VARIATION AND SYSTEMATICS IN THE _KINOSTERNON SCORPIOIDES_

AND _K. LEUCOSTOMUM_ COMPLEXES (REPTILIA: TESTUDINES:

KINOSTERNIDAE) OF MEXICO AND CENTRAL AMERICA

by

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To the Graduate Council of The University of Utah:

I have read the dissertation of James Frederick Berry in its final form and have found that (1) its format, citations, and bibliographic style are consistent and acceptable; (2) its illustrative materials including figures, tables, and charts are in place; and (3) the final manuscript is satisfactory to the Supervisory Committee and is ready for submission to the Graduate School.

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ABSTRACT

Phenetic relationships among populations of the mud turtles of the _Kinosternon_ _scorpioides_ and _K_. _leucostomum_ complexes in México and Central America were examined using multivariate statistical techniques.

Thirty-one mensural and five qualitative characters were measured on the external surfaces of 3,062 adults of the two species complexes. The geographic ranges of the species complexes were divided by river drainage into populations for statistical analyses. Fifty-eight populations were defined for the _K_. _scorpioides_ complex, and 22 for _K_. _leucostomum_.

Each complete statistical analysis included a multiple discriminant analysis, a canonical analysis, and a phenetic distance (D^2) analysis. Six complete analyses were run, one each on males and females of: (1) _K_. _integrum_ and its closest relatives; (2) _K_. _scorpioides_; and (3) _K_. _leucostomum_. Mensural data were standardized for size by dividing each character by carapace length; a comparison of ratio _vs_. regression standardization in _K_. _leucostomum_ analyses revealed no statistically significant differences in the results obtained.

Characters selected by the discriminant analyses and their functional significance are discussed. A highly intercorrelated character complex is described which suggests relatively high, wide carapaces

tend to be associated with extensive plastrons. It is hypothesized that this character complex is a terrestrial adaptation associated with seasonal aquatic environments; a test using a multiple regression analysis of environmental variables against relative plastral area confirms the hypothesis.

Females of all taxa tend to have more globular shells, more extensive plastrons, and less emarginate anal notches than males.

Canonical and distance analyses suggest that _K_. _integrum_ is closely related but phenetically distinct from two undescribed species from Sonora and Sinaloa, and Oaxaca, México. A population from the Río Purificación in coastal Jalisco is phenetically distinctive, but _integrum_ populations are otherwise relatively homogeneous.

Kinosternon scorpioides consists of four phenetically distinct subspecies in México and Central America: (1) _K_. _s_. _cruentatum_ in southern México, Belize, and Guatemala; (2) _K_. _s_. _abaxillare_ in the Río Grande de Chiapas; (3) _K_. _s_. _albogulare_ in most of Central America above the Isthmus of Panamá; and (4) _K_. _s_. _scorpioides_ on the Isthmus of Panamá and northern South America.

The _Kinosternon leucostomum_ complex consists of one species, _K_. _leucostomum_, with two subspecies: (1) _K_. _l_. _leucostomum_ in Atlantic drainages of southern México to eastern Nicaragua; and (2) _K_. _l_. _postinguinale_ in Atlantic and Pacific drainages from the Río San Juan in Nicaragua, southward to northwestern South America.

Lists of synonymies, diagnoses, and discussions of taxonomic history are given for each taxon. Descriptions and discussions of geographic range and natural history are given for each species.

The following are proposed as logical and parsimonious distributional histories. The _Kinosternon scorpioides_ and _K. leucostomum_ complexes arose in northern Central America during mid-Cenozoic. A _scorpioides_ ancestor gave rise to _K. integrum_ which spread from southern Pacific Coastal México to the Mexican Plateau, and then to the northern Pacific Coast. _K. scorpioides_ dispersed throughout the Pacific Coast of Central America, entering Atlantic drainages in eastern México and Nicaragua, and entering South America at the closing of the Panamanian Isthmus. _K. leucostomum_ dispersed throughout Atlantic Central America and entered South America at the closing of the Isthmus of Panamá. The patterns of distribution of the species complexes are generally those expected of a xeric-adapted Pacific Coast form, and a mesic-adapted Atlantic Coast form.

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INTRODUCTION

Interest in the herpetofauna of Central and South America (contiguous land masses from México southward) has been considerable since the early nineteenth century when serious examination of New World faunas began. By the end of the nineteenth century, the herpetofauna of the area was better known than any outside the United States and Europe. During the twentieth century, interest in the herpetofauna of Central and South America has been second only to that of the United States. Smith (1971-1977) lists 10,398 citations dealing with Mexican herpetology.

Knowledge of the distribution, systematic relationships, and evolutionary history of the turtles of the kinosternid genus *Kinosternon* is incomplete in spite of the intense interest in the Central and South American herpetofauna in general. Identification of Central and South American *Kinosternon* is very difficult for most herpetologists, and most museum collections contain misidentified or unidentified specimens. Recent papers by Conant and Berry (1978), Iverson (1978b), and Iverson and Berry (MS) have dealt primarily with misidentified kinosternids in the herpetological literature on the southwestern U.S. and northern Mexico.

The genus *Kinosternon* has received little biological attention for several reasons: (1) the shells of kinosternids are often encrusted with mud, chemical precipitates from the water, and/or epizoic algae which obscure the external form of the shell; (2) all *Kinosternon* tend to look very much alike to the untrained eye; and (3) kinosternids are a singularly unpleasant group with which to work when they are alive, since all produce a highly odoriferous and unpleasant musk, most occur in stagnant backwaters or muddy ponds, and many are extremely pugnacious when handled. Other reasons for the inadequate knowledge of kinosternids are the reasons turtles in general are difficult to study: (1) most are aquatic and require special collecting equipment such that adequate series of specimens are rarely collected in the course of general herpetological surveys; and (2) turtles require more time and effort to collect, prepare, and transport than do most reptiles, and most herpetologists do not expend the appropriate time and energy.

Linnaeus (1766) described the first kinosternid, *Kinosternon scorpioides* (as *Testudo scorpioides*) from Surinam. During a flurry of activity in the mid-nineteenth century many European herpetologists (notably the Dumerils, Bibron, Bocourt, Gray, Günther, Boulenger, Wagler, and Spix) and a few Americans (Cope, Agassiz, and LeConte in particular) diligently examined available museum specimens, and described or commented on most of them. While many new names were proposed during this period, descriptions were based on inadequate comparative material in most cases, and most of the names proposed were eventually placed in synonymy with others. The only general treatise on the Kinosternidae ever undertaken, that of Siebenrock (1907), arose from the activity of this period.

In the United States, Leonhard Stejneger of the U.S. National

Museum worked for many years on turtles, but he died in 1943 having produced but two small papers on *Kinosternon* (Stejneger, 1925, 1941). Likewise, Norman Hartweg of the University of Michigan studied turtles for many years, but when he died in 1964 he had produced only two short papers on *Kinosternon* (Hartweg, 1934, 1938). Stejneger and Hartweg were hampered in the preparation of truly comprehensive reviews of the Kinosternidae by the inadequate series of Central and South American *Kinosternon* available to them. Since the late 1950's several U.S. museums have accumulated satisfactory comparative series of Central American *Kinosternon* from limited geographic areas, but it was chiefly through the efforts of J. M. Legler (University of Utah) in the 1960's that the first truly comprehensive series of Central American *Kinosternon* became available for study.

Several workers produced short papers on geographically restricted or peripheral taxa of Central and South American *Kinosternon* during and since the times of greatest activity of Stejneger and Hartweg (Freiberg, 1936; Müller and Hellmich, 1936; Schmidt, 1947; Hellmich, 1958; Medem, 1961; Legler, 1965, 1966; and Cunha, 1970). Comprehensive investigations which should ultimately clarify kinosternid taxonomy are underway by several recent workers (Iverson, 1976, MS; Iverson and Berry, MS; Berry and Legler, MS; Berry and Iverson, MS).

The present study is part of a more inclusive investigation of evolution in the Kinosternidae presently underway. It is designed as a comprehensive study of geographic variation and systematic relationships in two species "complexes" (i.e., each complex contains taxa which have variously been known as members of a single species; see also Mayr's 1969:400 definition). These two species complexes are the *Kinosternon scorpioides* complex (including *scorpioides*, *cruentatum*, *albogulare*, *panamensis*, and *integrum*), and the *K. leucostomum* complex (including *leucostomum*, *postinguinale*, and *spurrelli*). These two complexes were chosen because: (1) both are wide ranging (México to South America) polytypic species complexes; (2) the systematic relationships of the members of both complexes are poorly understood; (3) members of both complexes (in Central America, at least) are well represented in museum collections; and (4) in Central America the distribution of the *K. leucostomum* complex is generally Atlantic while that of the *scorpioides* complex is generally Pacific, which allows an extremely useful comparison of distributional patterns and adaptive strategies.

The systematic relationships among individually and geographically variable taxa such as *Kinosternon* can be properly deduced only by first analyzing variational patterns in large series of specimens representing the entire range of variation. The objectives of the present study are as follows:

> (1) to analyze mensural and qualitative data on large numbers of members of the *Kinosternon scorpioides* and *K. leucostomum* species complexes using multiple discriminant analyses to determine those characters or sets of characters which most effectively account for the patterns of geographic variation observed in external morphology, and to explain these patterns in terms of environmental selective pressures; and
>
> (2) to determine the precise phenetic relationships among populations in each species complex

using canonical and cluster analyses which consider variational patterns, and to use the results to erect accurate taxonomies for each. The phenetic relationships among populations will also be used to infer distributional and evolutionary histories insofar as such inferences are possible.

MATERIALS AND METHODS

Specimens of *Kinosternon scorpioides* and *K. leucostomum* from most of the known geographic range in México and Central America were examined in the present study.

The reliability of the analyses ranges from poor to good as a direct result of the number of specimens available. *K. spurrelli* (*leucostomum* complex) from northwestern South America are well represented in U.S. museum collections, and are considered in detail. Very few specimens of South American *K. scorpioides* (which occurs throughout northern and central South America) are available for comparative study, so the analysis of South American *scorpioides* is both general and speculative.

A total of 3,671 specimens of *Kinosternon* was examined in this study, of which 3,062 were used in the statistical analyses of geographic variation. Those not used in the statistical analyses were juveniles, aberrant, or incomplete specimens from which complete data could not be obtained. No effort was made to examine every available museum specimen, although the larger museum collections were examined in detail. Specimens from unusual, questionable, or peripheral localities were selectively examined from smaller collections.

Characters

The characters used in the analyses of geographic variation were selected according to the following criteria, in order of priority: (1) characters which could be easily and quickly measured on the external surfaces of whole, preserved specimens; (2) characters for which the method of measurement could be described with enough facility to assure accurate repeatability by future workers; and (3) characters used in the original descriptions or diagnoses of the taxa involved.

Characters which were analytically redundant were not used. For example, the length of the abdominal scute and the length of the fixed portion of the plastron were not both used as characters since the measurement of both is essentially identical in the taxa studied (see Sokal, 1965; and Sneath and Sokal, 1973 for reviews of the effects of correlated characters in statistical analysis).

Color and pattern were noted in this study, but were found inadequate for statistical analysis for the following reasons: (1) color and pattern are difficult to quantify objectively; (2) unnatural variation in color and pattern frequently occurs in improperly or non-uniformly prepared specimens; and (3) color and pattern tend to become obscured and eventually lost in older, larger individuals. Notes on color and pattern were maintained on specimens of known uniformity of preservation (mostly University of Utah specimens) and will be discussed in later sections. The procedure for examining color and pattern was combined with observations on integumentary structures, and was standard. Mud, algae, and chemical precipitates were carefully scrubbed from the carapace and plastron, and color and pattern noted. The head and neck regions were wiped with a damp cloth to prevent glare, and the following noted: (1) degree and nature of mottling or spotting; (2) presence and nature of striping; (3) color; (4) shape of the dorsal head shield; (5) number and size of gular barbels; (6) number and nature of neck and tail papillae; (7) presence or absence of "clasping organs" (patches of specialized roughened scales on the posterior thigh and leg, see Legler, 1965; Mahmoud, 1967; Lardie, 1977); and (8) presence or absence of a terminal, horny claw on the tip of the tail.

All measurements were taken to the nearest 0.1 mm (rounded to the nearest 1.0 mm for statistical analysis) with standard 150 mm dial calipers, or 1 m vernier calipers.

Descriptions of the characters used follow. Members of the *K. leucostomum* complex generally lack an anal notch or carapacal keels as adults, so these characters were measured on *K. scorpioides* complex members only.

1. Carapace Length (CL). Linear measurement from anteriormost to posteriormost points on carapace (rarely at midline) measured with outside jaws of calipers lying in a frontal plane which intersects the anterior and posterior margins of the carapace, and is perpendicular to midsagittal plane (Fig. 1B). Differs from Iverson's (1977) measure in which jaws of calipers lie in midsagittal plane.

2. Greatest width of carapace (CWN). Expressed as number of marginal scute at widest point on carapace (e.g., M7). Marginal scutes numbered consecutively from 1-11, anterior to posterior (usually with 11 marginals, rarely 12, Fig. 2; no attempt was made to correct for rare anomalous specimens).

3. Carapace width, anterior (CWA). Measured at level of posterior border of anterior plastral lobe (usually at level of mid-M5); jaws of calipers held perpendicular to longitudinal axis of shell (Fig. 1B).

4. Carapace width, posterior (CWP). Measured at level of mid-M8, at approximate level of mid-femoral scutes (Fig. 1B); jaws of calipers held as in (3) above.

5-10. Lengths of interlaminal seams of plastron at midline; (5) gular length (GUL), (6) humeral length (HUL), (7) pectoral length (PEL), (8) abdominal length (ABL), (9) femoral length (FEL), and (10) anal length (ANL) (Fig. 1A). Where seams did not meet precisely at midline, mean length was used.

11. Depth of anal notch (NOT). Maximal linear length of posterior plastral lobe was measured from point at which interfemoral seam meets posterior hinge, to posteriormost point on free edge of plastron (jaws of calipers held approximately in plane of plastron, perpendicular to midline). Anal notch depth is difference between maximal length of posterior lobe, and sum of FEL (9) and ANL (10). (Fig. 1A).

12. Gular scute width (GUW). Maximal width measured at intersection of gular-humeral seam and free edge of anterior plastral lobe (Fig. 1B).

13. Humeral-pectoral seam width (HPW). Plastral width at intersection of humeral-pectoral seam and free edge of anterior plastral lobe (Fig. 1B).

14. Anterior hinge width (AHW). Plastral width at posterior

border of pectoral scutes (i.e., at posterior border of anterior hinge). Measured at same level as CWA (4) above (Fig. 1B).

15. Posterior hinge width (PHW). Posterior plastral lobe width measured at anterior border of posterior lobe (Fig. 1B).

16. Transfemoral width (TFW). Plastral width at mid-femoral scute. Measured at same level as CWP (5) above; usually widest point on posterior plastral lobe (Fig. 1B).

17. Femoral-anal seam width (FAW). Plastral width at intersection of femoral-anal seam and free edge of posterior plastral lobe (Fig. 1B).

18-20. Lengths of central scutes 1, 3, and 5 (C1L, C3L, C5L). Measured at the midline.

21. Anterior width of first central scute (C1A). Measured at points common to C1, first pleurals (P1), and marginals (either M1 or M2).

22. Posterior width of first central scute (C1P). Measured at points common to C1, C2, and P1.

23. Width of third central scute (C3W). Measured at points common to C3, P2, and P3 (i.e., at most lateral points of C3).

24. Width of fifth central scute (C5W). Measured at lateralmost points of contact between C5, P4, and marginals (M10 or M11).

25. Axillary scute length (AXL). Maximal linear measurement from anteriormost to posteriormost points on left side (Fig. 1B).

26. Inguinal scute length (INL). Maximal linear measurement from anteriormost to posteriormost points on left side (Fig. 1B).

27. Shell height (SHT). Maximal linear height (depth) of shell,

measured from point at middle of abdominal scute (or between points at middle of bridge on right and left sides if abdominal scute was concave) to highest point on carapace at anterior one-third of C3. Jaws of calipers were held perpendicular to longitudinal axis of shell.

28. Bridge length (BRL). Least linear longitudinal length of bony bridge, measured by inserting outside jaws of calipers into axillary and inguinal regions. Measured on left side only (Fig. 1A).

29. Head width (HW). Measured at posterior border of tympanum (not necessarily the widest part).

30-31. Degree of lateral and central carapacal keeling (DKL), DKC). A subjective but consistent estimate of relative height and distinctiveness of longitudinal keeling as estimated by eye. Varied from 0 (= no visible keeling) to 4 (= keeling maximal).

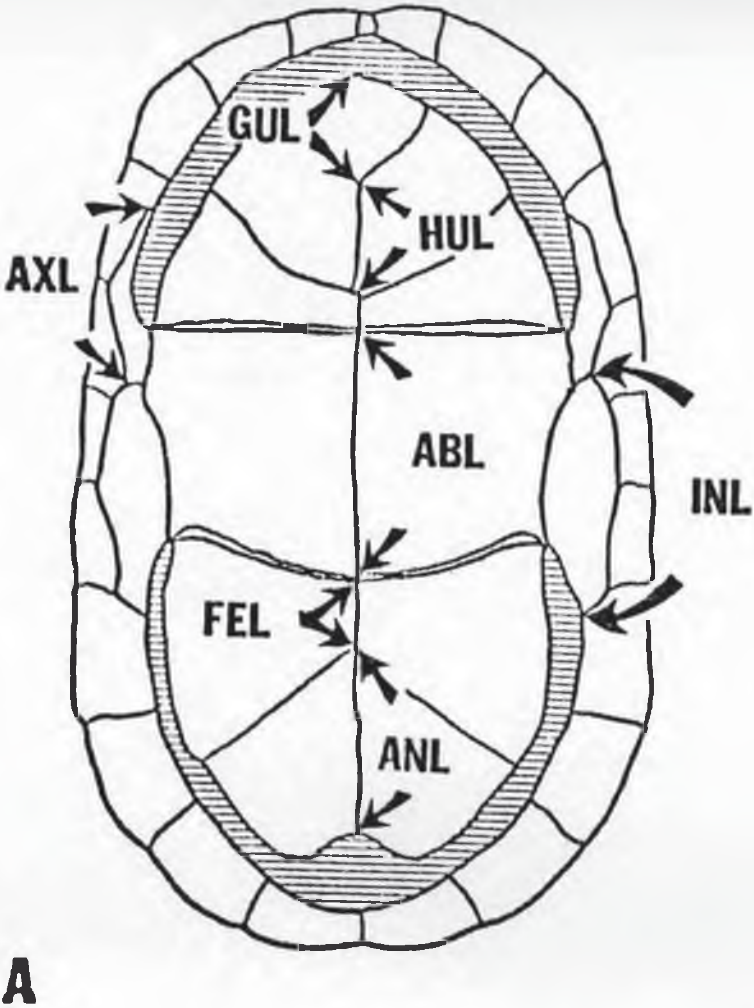
32. Presence of supernumerary inframarginal scutes (SIM). Usually extra inguinal scutes. Scored as follows: 2 = present on both sides; 1 = present on one side only; and 0 = absent on both sides.

33. Axillary and inguinal scutes in contact? (AIC). Scored as follows: 2 = contact on both sides; 1 = contact on one side only; and 0 = no contact on either side.

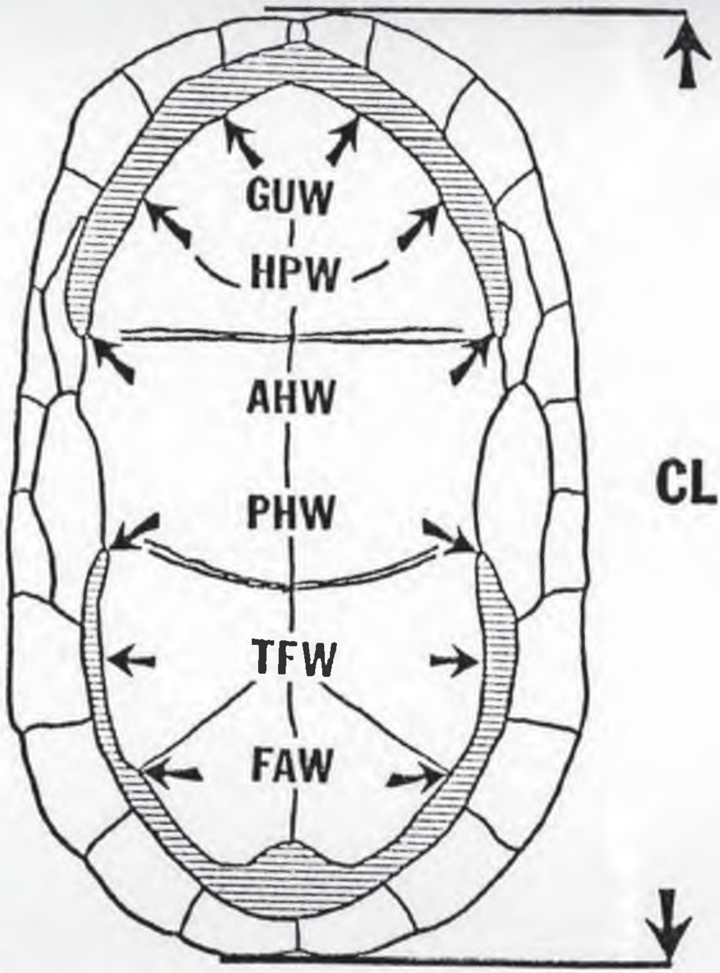
34. First central scute in contact with second marginal? (M2C). Scored as in 33 above.

35. Tenth marginal scutes higher than eleventh? (M11). Scored as follows: 2 = M10 higher on both sides; 1 = M10 higher on one side, but equal to or lower than M11 on the other; and 0 = M10 lower than or equal to M11 on both sides.

Figure 1. Drawing of the plastron of Kinosternon integrum (UU 7840 ♂) showing method of several measurements used in this study.

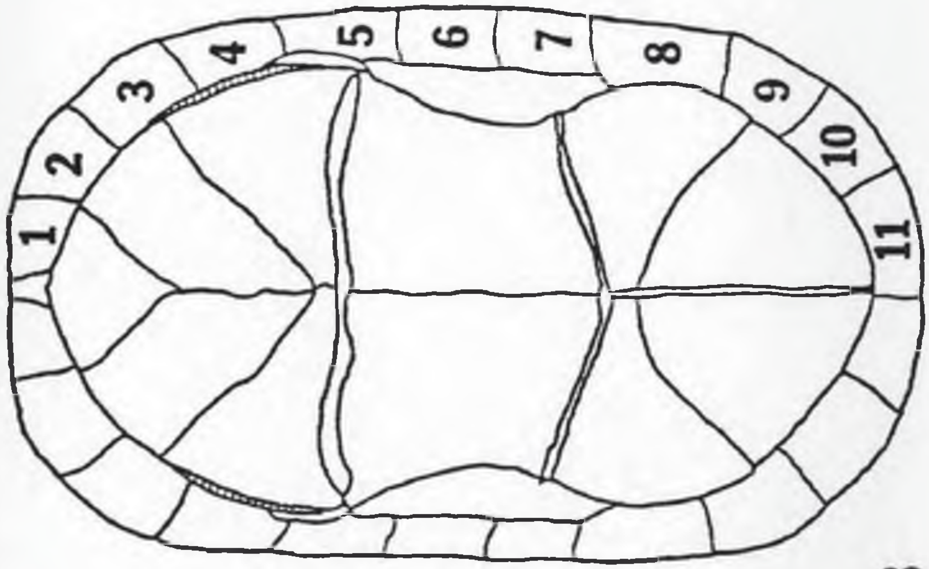


A

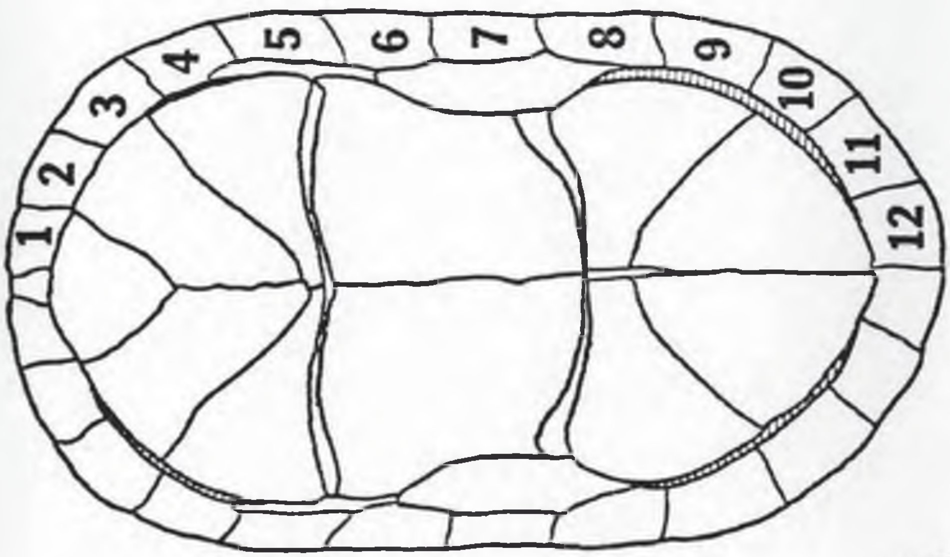


B

Figure 2. Drawings of the plastrons of *Kinosternon scorpioides* contrasting a specimen with twelve marginal scutes (A; UU 7246 ♂) to one with the normal eleven (B; UU 7342 ♂).



B



A

Definitions of Populations

For the purpose of statistical analysis, the geographic ranges of the K. scorpioides and K. leucostomum species complexes were subdivided into populations, the limits of which corresponded chiefly to river drainage systems. The populations thus formed were treated statistically as homogeneous but geographically discrete biological populations, although their composition was frequently based on subjective or arbitrary judgments such that they were only crude approximations of real biological populations.

The process by which populations were designated involved two steps. (1) All localities from which specimens had been examined were plotted on drainage system maps (Figs. 3-8). (2) Since Kinosternon tend to be restricted in their distribution to major river drainage systems, the geographic ranges of the K. scorpioides and K. leucostomum complexes were partitioned according to major river drainages.

If the number of specimens from a particular river system was very small, the specimens were often combined with those from an adjacent system and all specimens were treated as a single population (e.g., K. scorpioides from all northern Gulf of México drainages were treated as a single population). However, specimens from adjacent river systems were not combined unless it could be established that an opportunity existed for regular dispersal between the two river systems (e.g., via seasonal lowland swamps). Conversely, larger drainage systems were divided into smaller sections if sample sizes of specimens were large (e.g., the Río Balsas basin was divided into upper, middle, and lower sections).

The boundaries of the populations formed by this process are shown in Figs. 3-8. The extent to which these populations approximate real biological populations varies. In areas where the lower portions of adjacent river systems are periodically or permanently connected by swamps, lakes, streams, or even estuaries, the opportunity for gene flow is high. Populations on the northern Pacific Coast of México, most of the Gulf Coast of México, and the Caribbean Lowlands of most of Central America can be thus characterized. On the Pacific Coast of southern México and Central America, the coastal lowlands tend to be quite narrow and discontinuous, and *Kinosternon* populations are more nearly discrete.

Definitions and descriptions of geographic areas which delimit the populations used in the analyses are in Tables 1 and 2. The names and terms applied to river systems are those of Tomayo (1946, 1964). Terminology used for physiographic or geologic formations are those of West (1964). Since the geographic ranges and the manner in which populations were delineated differ, those for the *scorpioides* and *leucostomum* complexes are listed separately. In several instances, populations were further subdivided after initial analysis, and these are designated by an "A" or "B" following the numerical designation for *scorpioides* complex members, and "1" or "2" following an alphabetical designation for *leucostomum* complex members. In the one case where two species from the same species complex are sympatric (i.e., *K. alamosae* and *K. integrum*) specimens of the two species are treated as if belonging to geographically discrete populations. In general, populations are numbered from north to south, and from west to east. The names of states in Mexico, and countries elsewhere in Central and South America in which each population occurs follow each population in parentheses.

Statistical Techniques

Techniques for the analysis of geographic variation vary considerably in their degree of complexity and sophistication (see recent reviews by Gould and Johnston, 1972; and Sneath and Sokal, 1973). There is general agreement that multivariate techniques (i.e., many characters considered simultaneously) are superior to univariate techniques, primarily because variation tends not to be the result of one or a few characters adapted to one or a few environmental parameters, but many characters adapted to all environmental parameters to which the organism is in contact (Sokal and Rinkel, 1963).

Two general, non-independent types of multivariate analysis were used in the present study, as described below.

(1) Determination of new axes. A data matrix of correlated characters can be distilled into a new set of uncorrelated axes. In the type of analysis used in this study, axes subsequent to the first are orthogonal. Multiple discriminant analysis (MDA) is the preferred technique for the analysis of geographic variation in closely related groups (Gould and Johnston, 1972; Sneath and Sokal, 1973). In MDA, the axes are arranged in such a way that they maximize separation between groups in a stepwise fashion; the first axis (= classification

function) accounts for more variation than the second, and so forth for as many steps as are permitted. Reviews of MDA techniques and mathematical procedures are in Cooley and Lohnes (1971), Blackith and Reyment (1971) and Sneath and Sokal (1973). This technique has been used in numerous recent analyses of variation (see reviews in Gould and Johnston, 1972; and Zimmerman and Ludwig, 1975). Iverson (1977, 1978a) used similar techniques in analyses of variation in kinosternid turtles.

(2) Distance analyses. These techniques generate a measure of relative distance between sample means as projected on a Euclidean plane (see reviews in Sneath and Sokal, 1973; and Goodman, 1974). Mahalanobis' D^2 is the most popular distance measure (see Metter and Pauken, 1969; and Pauken and Metter, 1971; Feuer, 1966 used D^2 in analyzing variation in Snapping Turtles). This measure is a natural by-product of MDA since D^2 can be calculated by multiplying the difference between discriminant function vectors by the difference between character means of the two groups being considered (Blackith and Reyment, 1971; Dixon, 1974).

The MDA computer program selected for use in the present study was BMD07M (Dixon, 1974). This program is readily available to most workers, and has been used effectively in analyses of variation (Jackson, 1973; Lee, 1977; but see Lachin and Schacter's, 1974, criticisms of BMD07M, and Gibson's 1977 criticism of Jones, 1976 use of BMD07M).

BMD07M first generates sets of linear classification functions using independent variables chosen step-wise, beginning with variables with the largest F-values and ending when F-values fall below 0.01, or when the step corresponding to the maximum number of characters used in the analysis is reached. The variables chosen represent, in order, those with the greatest discriminatory power. Thus, all variables which add to the effectiveness of the discriminant function are included.

D^2 values from group mean to group mean are calculated but not presented by BMD07M. These values can be retrieved by calculating from the table of F-values presented after the final step in the MDA. These D^2 values are then arranged in a "Dendrograph" to demonstrate phenetic relationships, using a program devised by McCammon and Wenninger (1970).

The probability that each individual specimen belongs to each geographic group in the analysis (including the one to which it was initially assigned) is also calculated. With caution, these probabilities can be used to assess the degree of "overlap" between two populations by determining the number of "mistakes" (i.e., number of specimens which originated from one population, but were placed in another population by the MDA). The number of specimens from each population which were placed in the "correct" population as well as the number placed in "incorrect" populations is presented for each analysis.

A canonical analysis was performed with each MDA (see Seal, 1964; Blackith and Reyment, 1971; Cooley and Lohnes, 1971; Sneath and Sokal, 1973; and Dixon, 1974 for detailed mathematical explanations). A plot of population mean values on the first two canonical variates provides visual representation of phenetic relationships among populations.

Other useful statistics calculated by BMD07M include group and overall means for each character, standard deviations of each character for each population, and within populations correlation matrices.

MDA analyses were performed in series of two runs; once on adult males, and once on adult females. Comparison of the results of the two runs allows determination of sexual dimorphism in the characters used, and sexual differences in patterns of geographic variation. Complete MDA analyses were performed twice on the *Kinosternon leucostomum* complex, once each using different data standardization techniques (see below). Complete MDA series were performed independently on *K. scorpioides*, and *K. integrum* and its closest relatives.

BMD07M has no provision for missing data. When a particular data point was missing, a program utilizing subroutine MISDAT of the Univac Stat-Pack series (Univac, 1972) was used to approximate the missing data. If a particular specimen lacked more than a few characters, or if it was judged to be pathologically abnormal, it was not used in the MDA analyses.

A multiple regression analysis used later in the analyses utilized program BMD02R (Dixon, 1974).

Analyses were not performed on immature animals. Individuals were judged to be mature if their carapace length exceeded that of animals found to be mature by inspection of gonads. Individuals of *K. leucostomum* from Panamá were found to mature at CL of 80 mm (females) and 100 mm (males) by Moll and Legler (1971), and *leucostomum* complex members whose CL exceeded these were considered mature in this study. *K. scorpioides* complex members were found to vary considerably in the size at which they reach sexual maturity. I found that a female *K. scorpioides* from the Yucatan Peninsula 90 mm in CL was sexually mature, but females of 110 mm and 120 mm CL from Cabo Gracias a Dios, Nicaragua, and Puntarenas Province, Costa Rica respectively were both immature. For simplicity, I assumed *K. scorpioides* and *K. integrum* males which appeared superficially to be mature (i.e., possessed appropriate secondary sexual characteristics, primarily a long, prehensile tail) and whose carapace lengths exceeded 100 mm were mature; while all females with CL in excess of 100 mm were considered mature. This method undoubtedly omitted many mature animals and included many which were immature, but probably achieved the objective of avoiding the expression of a juvenile morphotype as part of the adult range of variation.

Data Standardization

The analyses used in this study contained no provision for standardization of data, so it was necessary to standardize data prior to analysis. Such standardization is necessary in animals with continuous growth to correct for differences in absolute size of animals. Without standardization, results of multivariate analyses are measures of differences in body size rather than geographic variation since size alone will account for practically all measurable variation.

Techniques for standardizing non-linear size dependent characters normally use forms of the allometry formula (see reviews in

Corruccini, 1972; and Sneath and Sokal, 1973). A much simpler approach to size standardization is the use of ratios (Metter, 1967). Character values are usually divided by some measure of the absolute size of the organism (carapace length in this study). Ratios have been used as input variables in multivariate analysis by several recent workers (Feuer, 1966; Moulton, 1973; Iverson, 1978a; Berry, *in press*). Criticisms and defense of the use of ratios have appeared in the recent literature (Sokal, 1965; Jackson, 1973; Atchley et al., 1976; Corruccini, 1977; Hills, 1978; Dodson, 1978; Albrecht, 1978; Atchley and Anderson, 1978; and Atchley, 1978). Criticisms fall into three general categories: (1) most multivariate procedures assume normally distributed data, but there is no evidence that ratios are normally distributed; (2) unless the regression line of the variable regressed on its denominator passes through the origin, ratios do not constitute a linearly size-corrected variable; and (3) ratios have an associated degree of unanticipated and theoretically mysterious "spurious correlation" (see Atchley et al., 1976).

In order to compare the effects of ratio use to the use of residual values from regression analysis (as recommended by Atchley et al., 1976) as input variables in multivariate analysis, series of MDA analyses of *K. leucostomum* complex members were each run twice. In the first MDA series, ratios were calculated (using a Fortran program written by the author) by dividing each mensural character for a particular specimen by CL for that specimen (i.e., $B_{ij} = A_{ij}/A_{i1}$, where i = specimen number and j = character number). Characters CWN, SIM, AIC, M2C, and M11 are counts or qualitative characters which require no standardization. A second identical series of MDA analyses was then run, except residual values (as calculated using subroutine GLH - General Linear Hypothesis - of the Univac Stat-Pack series, Univac, 1972) were used as input variables instead of ratios. Results of these analyses will be considered in a later section.

Figure 3. Geographic ranges of *Kinosternon alamosae* (dots) and *K. integrum* (triangles) in southern Sonora, southwestern Chihuahua, and northern Sinaloa, México. Star represents the type locality of *K. alamosae*.

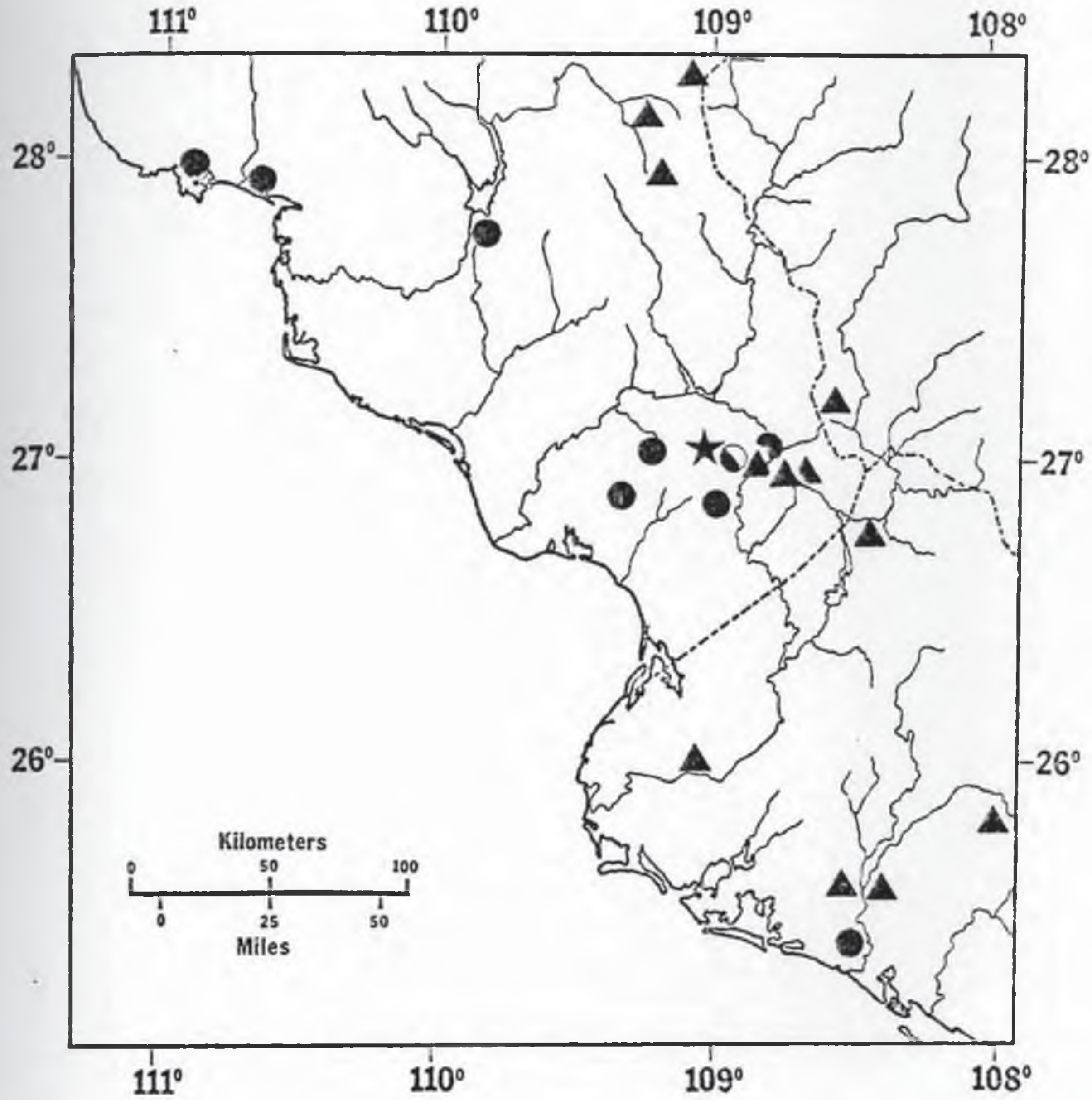

111°
110°
109°
108°
28°
27°
26°
Kilometers
0
50
100
0
25
50
Miles

Figure 4. The geographic ranges of Kinosternon integrum (dots), K. scorpioides (triangles), and K. oaxacae (squares) in northern and central Mexico. Populations as defined in the text are outlined by dotted lines.

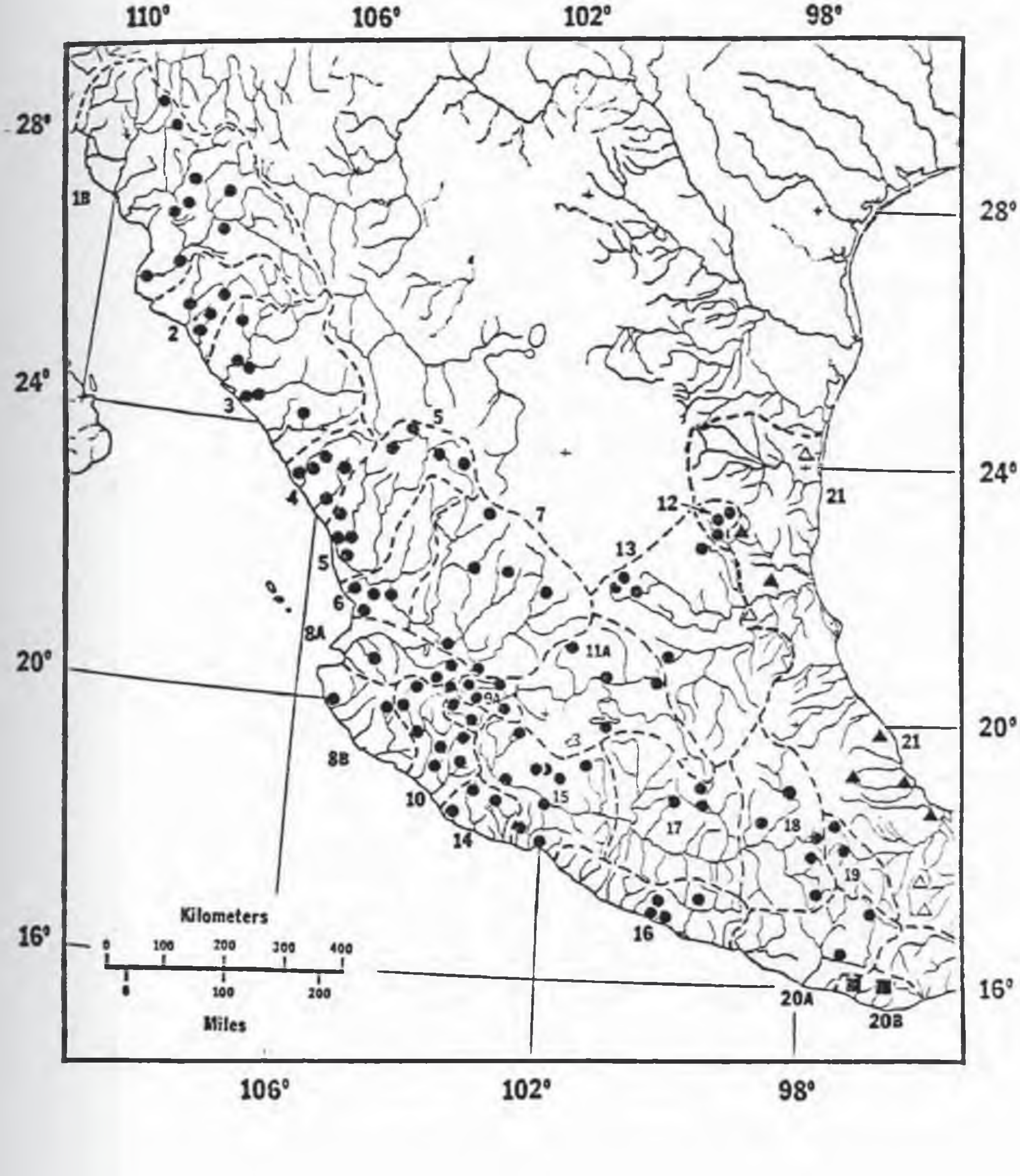

110°
106°
102°
98°
28°
24°
20°
16°
1B
2
3
4
5
6
7
8A
8B
9A
10
11A
12
13
14
15
16
17
18
19
20A
20B
21
Kilometers
0
100
200
300
400
Miles
0
100
200

Figure 5. Geographic range of Kinosternon scorpioides in southern Mexico and Central America. Dots are localities from which specimens were examined, circles are literature records. Populations as defined in the text are outlined by dotted lines.

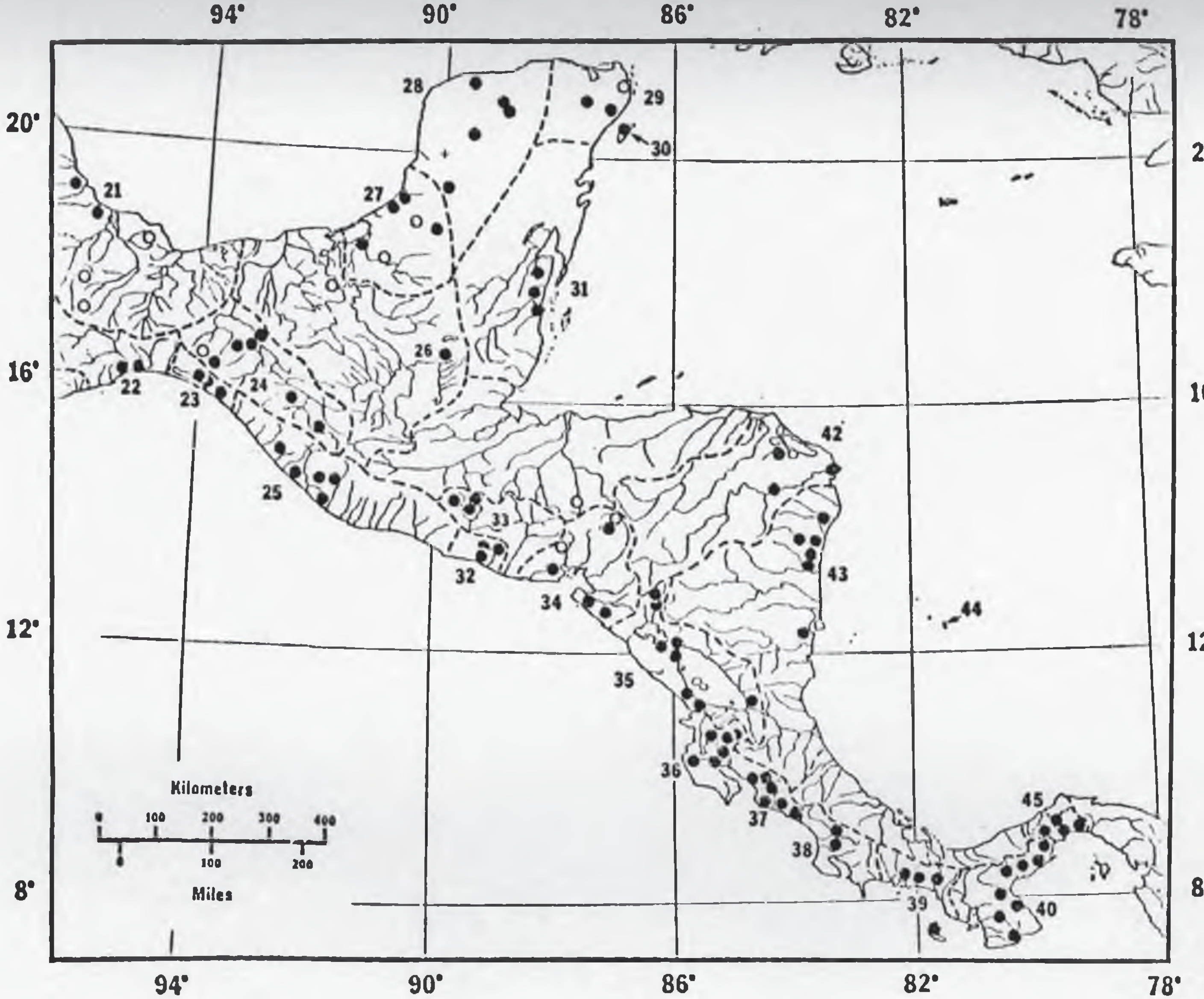
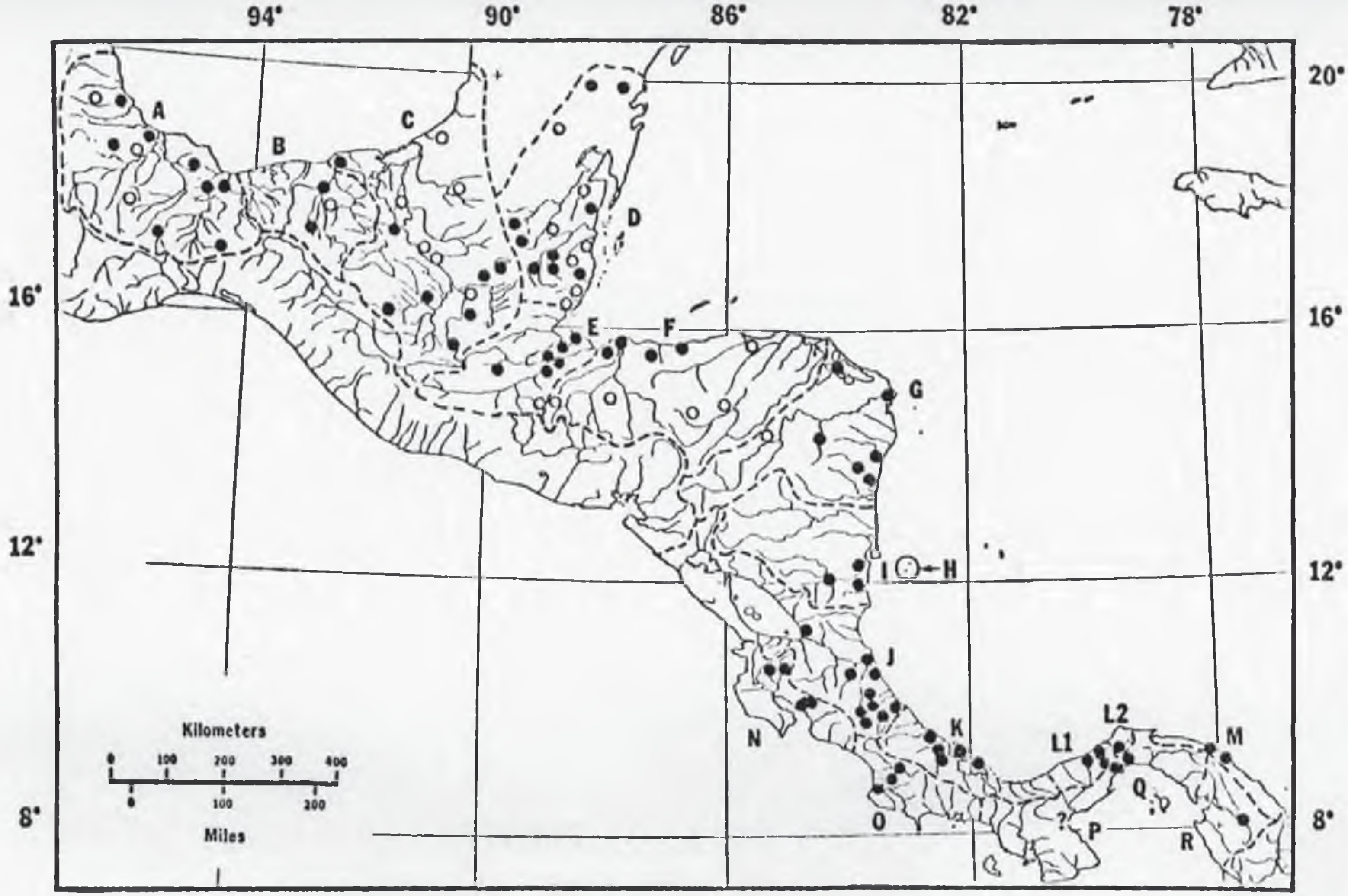

94°
90°
86°
82°
78°
20°
16°
12°
8°
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
42
43
44
45
Kilometers
0
100
200
300
400
Miles
0
100
200

Figure 6. Geographic range of *Kinosternon scorpioides* in South America. Dots are localities from which specimens were examined, circles are literature records, triangle is the type locality of *K. s. serei*, square is the type locality for *K. s. pachyurum*, and star is the type locality for *K. s. carajasensis*.

80°
70°
60°
50°
40°
10°
0°
10°
20°
30°
10°
0°
10°
20°
30°
80°
70°
60°
50°
40°

Figure 7. Geographic range of *Kinosternon leucostomum* in southern México and Central America. Dots are localities from which specimens were examined, circles are literature records. Populations as defined in the text are outlined by dotted lines.


94°
90°
86°
82°
78°
20°
16°
12°
8°
A
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C
D
E
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H
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J
K
L1
L2
M
N
O
P
Q
R
?
Kilometers
0 100 200 300 400
0 100 200
Miles

Figure 8. Geographic range of _Kinosternon leucostomum_ in South America. Dots are localities from which specimens were examined, circles are literature records. Populations as defined in the text are outlined with dotted lines.

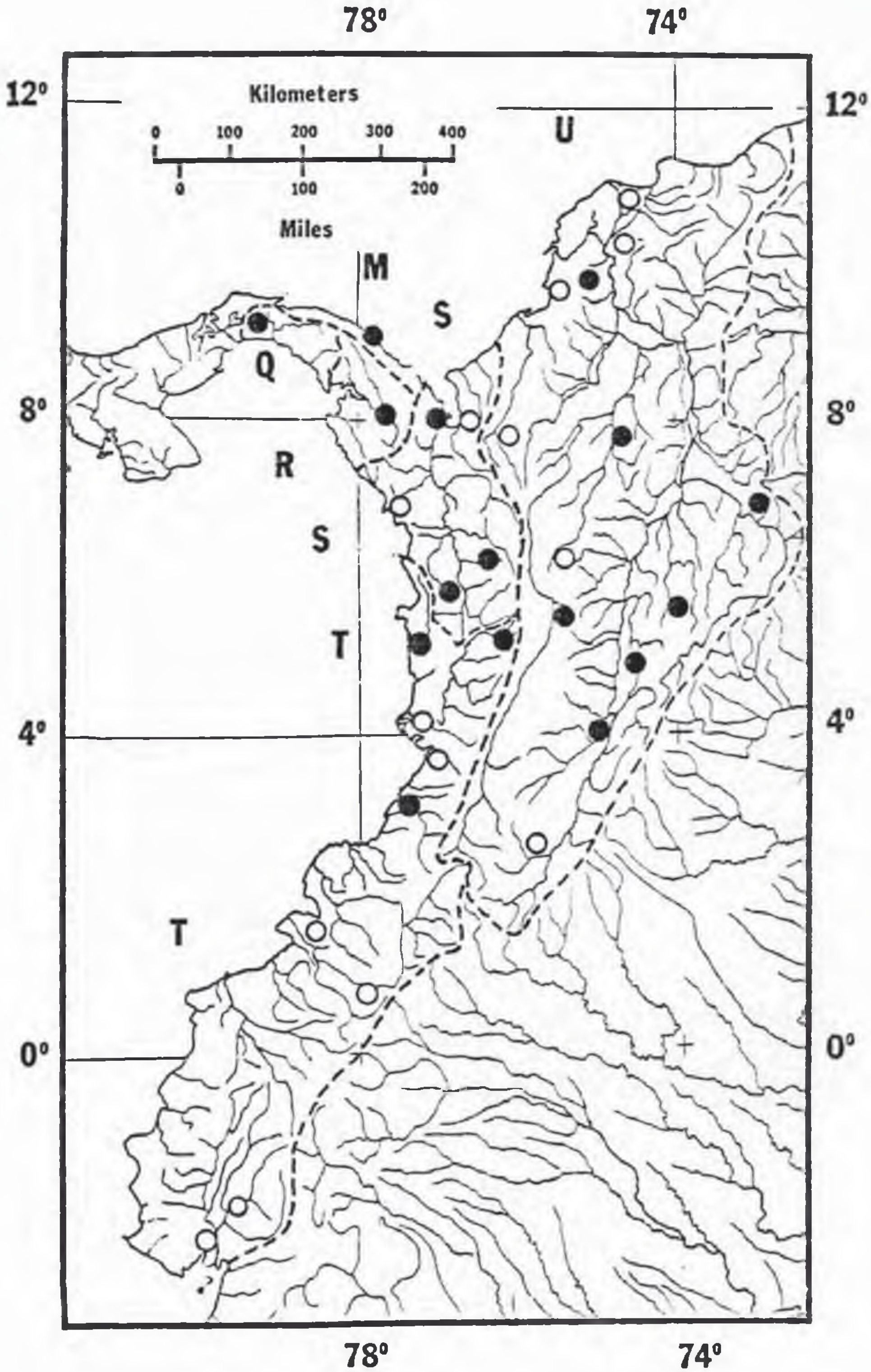

78°
74°
12°
Kilometers
0
100
200
300
400
0
100
200
Miles
U
M
S
Q
8°
R
S
T
4°
T
0°
78°
74°

Table 1. Populations of *Kinosternon scorpioides* complex members used in the statistical analyses.

1A. Range of *K. alamosae*; lower Río Yaqui (south of Cerro de Guaymas) to Rio Sinaloa (Pacific), inclusive (Sonora, Sinaloa).

1B. Lower Río Yaqui (south of Cerro de Guaymas) to Río Fuerte (Pacific), inclusive (*K. integrum*) (Sonora, Sinaloa, Chihuahua).

2. Ríos Sinaloa to Mocorito (Pacific), inclusive (Sinaloa).

3. Ríos Culiacán to Piaxtla (Pacific), inclusive (Sinaloa).

4. Ríos Presidio to del Baluarte (Pacific), inclusive (Sinaloa).

5. Ríos Acaponeta to San Pedro (Pacific), inclusive (Sinaloa, Nayarit, Durango).

6. Río Grande de Santiago (Pacific) upstream to confluence with Rio Bolanos, to Río Chila, inclusive (Nayarit).

7. Upper Río Grande de Santiago upstream from confluence with Río Bolanos to confluence with Río Verde, including all tributaries of Ríos Bolanos, Juchipala, and Verde (Jalisco, Zacatecas, Aguascalientes).

8A. Río Ameca-Mascota basin (Pacific), inclusive (Nayarit, Jalisco).

8B. Pacific coastal drainages from Cabo Corrientes to Río Cihuatlán, inclusive (Jalisco, Colima).

9A. Lago de Chapala drainage basin (Pacific) including Río Grande de Santiago upstream from confluence with Río Verde, and Río Lerma downstream from confluence with Río Duero (Jalisco, Michoacán).

9B. Laguna de Atotonilco Valley south to Laguna Zapotlán, inclusive (Jalisco).

10. Río Armería to Río Coahuayana basins (Pacific), inclusive (Jalisco, Colima, Michoacán).

11A. Río Lerma basin (Pacific) upstream from confluence with Río Duero (Michoacán, Guanajuato, Querétaro, México).

11B. Internal drainage of the Valley of México (Distrito Federál, México).

12. Río Guayalejo (Atlantic) above confluence with Río Tamesí (Tamaulipas).

13. Río Pánuco basin (Atlantic), including the Río Tamuín basin upstream from its confluence with Río Tampaón, and Río Moctezuma upstream from its confluence with the Río Pánuco (San Luis Potosí, Querétaro, Guanajuato).

14. Ríos Coalcomán and Nexpa (Pacific), inclusive (Michoacán).

15. Lower Río Balsas basin (Pacific), including all tributaries upstream to confluence with Río Mexcala (Michoacán, Guerrero).

16. Ríos Ixtapa to Copala (Pacific), inclusive (Guerrero).

17. Río Mexcala basin (middle section of Río Balsas) upstream from confluence with Río Balsas to confluence with Río Amacuzac (Pacific), inclusive (Guerrero, Morelos, México).

18. Upper Río Mexcala basin (upper section of Río Balsas) upstream from confluence with Río Amacuzac (Guerrero, Puebla, Oaxaca).

19. Río Santo Domingo (Río Papaloapan basin, Atlantic) upstream from confluence with Río Tonto (Puebla, Oaxaca).

20A. Río Verde basin (Pacific), inclusive (Oaxaca).

20B. Known range of _K_. _oaxacae_, Río Colotepec to Tonameca (Pacific), inclusive (Oaxaca).

21. Ríos Soto la Marina to Coatzacoalcos (Atlantic), inclusive, but excluding Río Guayalejo (Tamesí), Río Moctezuma (Pánuco), Río Tamuín (Pánuco) upstream of confluence with Río Tampaón, and Río Santo Domingo (Papaloapan) (Tamaulipas, Veracruz, San Luis Potosí).

22. Ríos Tehuantepec to Ostuta (Pacific), inclusive (Oaxaca).

23. Ríos Tepanatepec to Pijijiapan (Pacific), inclusive (Oaxaca, Chiapas).

24. Río Grande de Chiapas (Grijalva; Atlantic) upstream from confluence with Presa Malposo (Río Mezcalapa) (Chiapas, Guatemala).

25. Ríos Coapa to Paz (Guatemala-El Salvador border, Pacific), inclusive (Chiapas, Guatemala, El Salvador).

26. Río Usamacinta basin (Atlantic), inclusive (Guatemala).

27. Ríos Candelaria to Chompotón (Atlantic), inclusive (Campeche).

28. Ríos Hontún to Lagartos (Atlantic), inclusive, including most of the interior and seasonal drainages (mostly sinkholes and ponds) on the northwestern Yucatan Peninsula (Yucatan, Campeche).

29. Internal drainages (mostly sinkholes and ponds) on northeastern Yucatan Peninsula (Quintana Roo).

30. Atlantic drainages on Isla Cozumel (20°25'N, 86°55'W) (Quintana Roo).

31. Ríos Hondo to Sarstún (Atlantic), inclusive (Belize, Guatemala).

32. Río Grande basin and Lage de Coatepeque (El Salvador).

33. Río Lempa basin and Lagos de Guija and Metapán (El Salvador, Guatemela, Hondiras).

34. Ríos Grande de San Miguel to La Virgen (Pacific), inclusive, including all drainages into Golfo de Fonseca (El Salvador, Honduras, Nicaragua).

35. Río San Juan basin (Atlantic) including Lagos de Managua and Nicaragua in the "Nicaragua Depression" physiographic region (Nicaragua, Costa Rica).

36. Río Tempisque basin to Río Barranca (Pacific), including all drainages of the Peninsula de Nicoya (Costa Rica).

37. Ríos Santa María to Coronado (Pacific), inclusive (Costa Rica).

38. Río Diquis basin (Pacific) (Costa Rica).

39. Río Coto basin (Costa Rica) to Río Tabasará (Panamá), inclusive, including all drainages into Golfo de Chiriqui (Pacific).

40. Ríos San Pablo to Caimito (Pacific), inclusive, including all drainages of the Peninsula de Azuero and Isla de Coiba (Panamá).

42. Río Patuca basin to Río Coco basin (Atlantic), inclusive, on northern portion of "Mosquito Lowlands" physiographic region (Honduras, Nicaragua).

43. Ríos Wawa to Punta Gorda (Atlantic), inclusive, forming southern portion of "Mosquito Lowlands" (Nicaragua).

44. Isla de San Andres (Atlantic) lying 202 km E of Nicaraguan mainland (12°36'N, 81°40'W) (Colombia).

45. The Panama Canal and its tributaries, to Río Chepo, inclusive (Canal Zone, Panamá).

46. Río Magdelena basin (Atlantic; Colombia).

47. Drainages into Ciénegas de Ocumare (Atlantic; Venezuela).

48. Island drainages of Trinidad (Atlantic).

49. Ríos Essequibo to Carrantija (Atlantic; British Guiana).

50. Lower Río Amazon basin (Atlantic; Brazil).

51. Río Grande del Norte basin (Atlantic; Brazil).

52. Ríos Napo and Pastaza (Atlantic), upper Amazon (Ecuador).

53. Río Ucayali (Atlantic), upper Amazon (Peru).

54. Río Paraná basin (Atlantic; Argentina).

Table 2. Populations of Kinosternon leucostomum complex numbers used in the statistical analyses.

A. Ríos Actopan to Coatzacoalcos (Atlantic), inclusive (Veracruz, Oaxaca).

B. Río Mescalapa-Grijalva basin (Atlantic), upstream from confluence with Río Usumacinto (Tabasco).

C. Río Usumacinta basin (excluding Río Mescalapa-Grijalva) to Río Chompotón (Atlantic), inclusive (Tabasco, Chiapas, Guatemala).

D. Atlantic drainages into Bahía de la Ascensión on eastern Yucatan Peninsula, southward to Moho River, inclusive (Quintana Roo, Guatemala, Belize).

E. Temash River to Río Motagua (Atlantic), inclusive (Belize, Guatemala).

F. Ríos Chamelecón to Ulúa (Atlantic), inclusive (Honduras).

G. Ríos Patuca to Cuculaya (Atlantic), inclusive (Honduras, Nicaragua).

H. Atlantic drainages of Corn Island (Isla del Maize) 71 km WNW Bluefields, Nicaragua (12°15'N, 83°00'W) (Nicaragua).

I. Ríos Prinzapolca to Rama (Atlantic), inclusive (Nicaragua).

J. Río San Juan basin (including Lagos de Managua and Nicaragua), to Río Banalte (Atlantic), inclusive (Nicaragua, Costa Rica).

K. Ríos Sixaola to Loabre (Atlantic), inclusive (Costa Rica, Panama).

L1. Río Indio (Atlantic), to the Panama Canal including all tributaries except Río Chagres (Panamá, Canal Zone).

L2. Río Chagres basin upstream from its confluence with the Panama Canal at Gamboa, Canal Zone.

M. Atlantic drainages east of Punta Manzanillo (Panama) to Cabo Tiburón (Panamá-Colombia border).

N. Ríos Tempisque to Savegre (Pacific), inclusive (Costa Rica).

O. Ríos Diquis to Dupi (Pacific), including drainages of the Peninsula de Nicoya (Costa Rica, Panamá).

P. Pacific drainages of the Peninsula de Azuero (Río de la Villa), Panamá.

_Q_. Goofy Lake, 5 mi NNW Tocumen, Panamá (9°05'N, 79°23'W).

_R_. Río Chucunaque-Tuira basin (Pacific), (Panamá).

_S_. Río Atrato basin, to Río León (Atlantic), inclusive (Colombia).

_T_. Río San Juan basin, south to Río Daule (Pacific), inclusive (Colombia, Ecuador).

_U_. Río Magdalena basin (Pacific), inclusive (Colombia).

RESULTS

The results of all statistical analyses, Tables 3-38, appear in Appendix 1.

Comparison of Ratio and Regression Standardization Techniques

Results of analyses of *Kinosternon leucostomum* using the two techniques of data standardization are presented as follows: correlation coefficients, Tables 3-6; number of specimens classified into each group by MDA analyses, Tables 7-10; summary tables of MDA analyses, Tables 11-14; plots of mean coordinates for each group, and comparisons of the relative dispersion of points around each mean on the first two canonical variates in Figs. 9-12; and dendrographs based on distance measures (Mahalanobis' D^2) generated by the MDA analyses in Figs. 13-16.

Atchley et al. (1976) found that correlations between characters in their simulated analyses were inexplicably higher when ratios were used as input variables. However, examination of correlation coefficients generated by the MDA analyses in this study tends to support Corruccini's (1977) claim that "spurious correlation" constitutes a minimal complication. The following mean correlation coefficients and variances for *leucostomum* analyses were calculated from the matrices in Tables 3-6: males (standardized by regression) $\bar{X}$=0.059,

s^2=0.20; males (ratios) $\bar{X}$=0.060, s^2=0.020; females (regression) $\bar{X}$=0.059, s^2=0.023; and females (ratios) $\bar{X}$=0.067, s^2=0.023. All of these means differ from zero at the 0.05 level of significance (Student's "t" test of H_0:$\bar{X}$=0 with d.f.=464, t=6.40, 6.48, 5.92, and 6.79 respectively; from Snedecor and Cochran 1967). However, the mean correlation coefficients between analyses using ratios did not differ at the 0.10 level from those using regression standardization (Student's "t" test of H_0:$\bar{X}_1$=$\bar{X}_2$ with d.f.=454; for males, ratio _vs_. regression, t=0.16; for females t=0.80).

Examination of Tables 7-19 reveals that, in spite of a number of minor differences, the MDA analyses tended to classify specimens in very similar patterns. The number of specimens classified "correctly" (i.e., classified in the same group to which they were assigned _a priori_) was nearly identical regardless of standardization technique. In the analyses of males using data standardized by regression and ratios respectively, 470 (72.4%) and 471 (72.6%) of 649 specimens were classified "correctly"; and in the analyses of females 334 (73.6%) and 337 (74.2%) of 454 specimens were classified "correctly."

Examination of Tables 11-14 reveals that the order in which variables were added to the MDA is nearly identical in regression _vs_. ratio based analyses. The five most "important" variables in the analyses of males, and the three most important in females (those with F > 10.0) are identical. There are some slight differences in order among the "less important" characters.

Plots of group means on the first two canonical axes (Figs. 9-12) further reinforce the basic similarities in results of the two standardization techniques. Aside from minor differences in orientation within clusters, the basic orientations are the same within analyses for each sex regardless of standardization technique. Some slight tendency for isolated or peripheral points to appear further separated from tighter clusters is evident in regression-standardized analyses.

Dendrographs based on D^2 values (Figs. 13-16) show more prominent differences between standardization techniques, but even these are considered minor. Some differences in branching sequences can be identified, for example, the sequence L-L2-Q-M-R-O in the males regression standardized analysis is replaced by L-L2-M-R-O-Q in the ratio-based analysis (note, however, that group Q is the only one to differ in relative position). Groups which appeared peripheral or isolated in the canonical plots vary somewhat in their relationships to more compact groups, reflecting the tendency for regression standardization to amplify larger distances. For example, populations A and B are more similar to each other (D^2=12.5) than to any other group in the male regression-based analyses (D^2=34.0), while group B in the ratio-based analysis appears closer (D^2=16.4) to the group D-E-F-C-G-I than to Group A (D^2=19.1). Group H (Corn Island, Nicaragua), which is isolated geographically as well as by the canonical axes, is closer to the sequence L-L2-M-R-O-Q in the male ratio-based analysis, but clusters with groups C, D, E, F, G, and I in the other analyses.

Interpretations of the relationships among particular groups, as well as between males and females, will be discussed in a later

Figure 9. *Kinosternon leucostomum* males, plots of population means on first (I) *vs*. second (II) canonical variates (data standardized by regression).

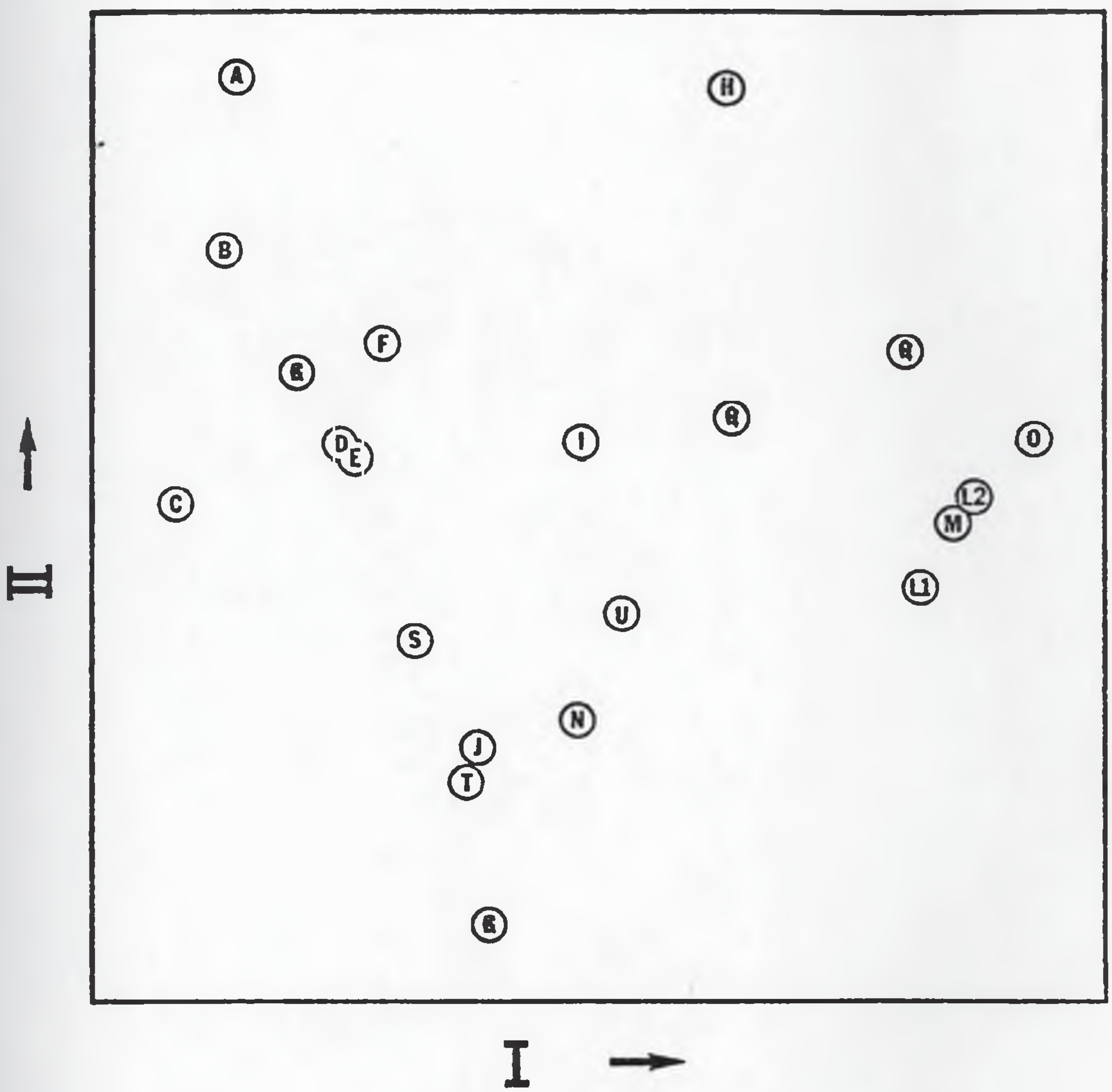
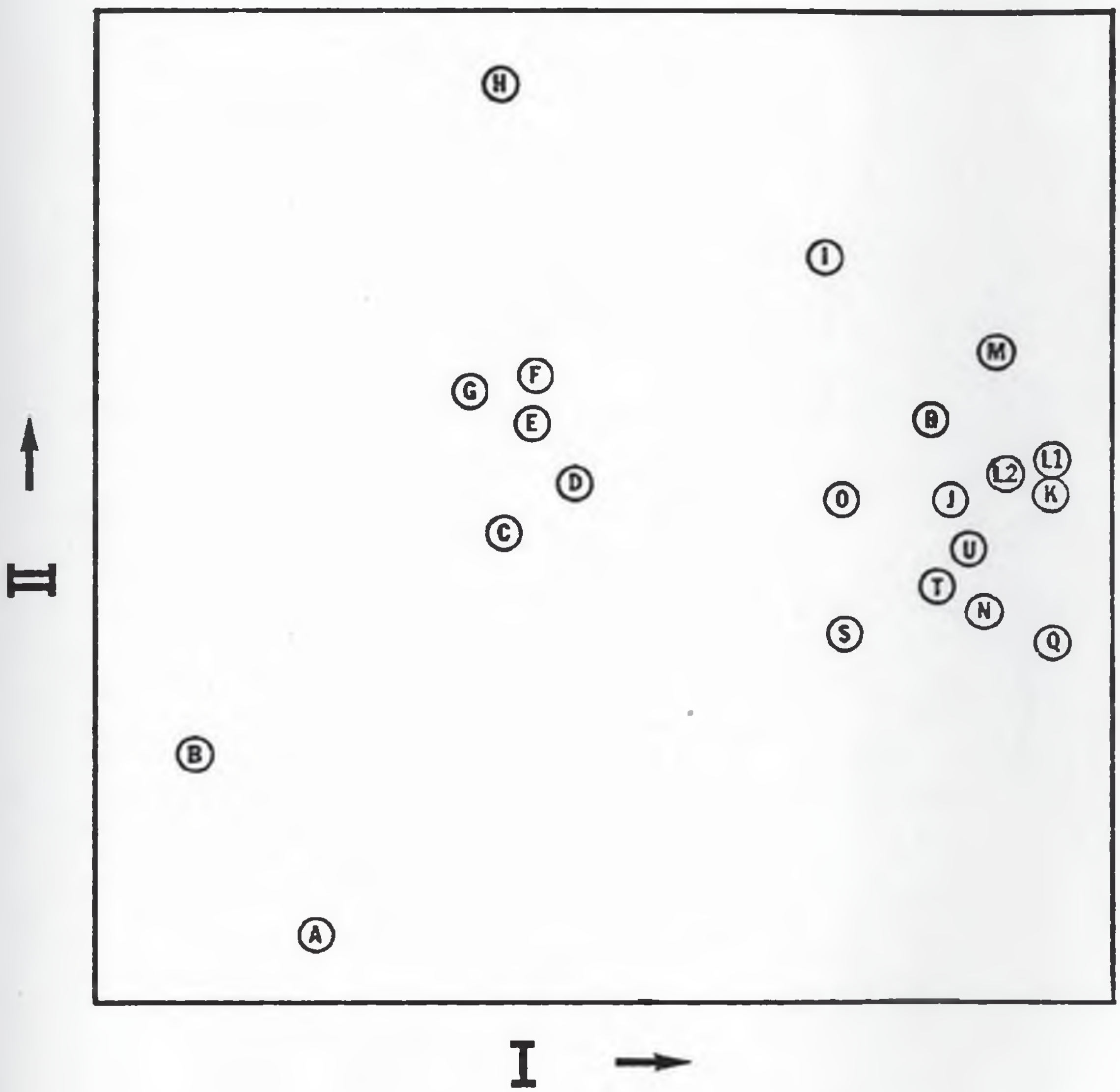

A
H
B
F
D
E
I
O
C
L2
M
L1
U
S
N
J
T
II
I

Figure 10. Kinosternon leucostomum females, plots of population means on first (I) *vs*. second (II) canonical variates (data standardized by regression).


H
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G
E
L1
L2
D
O
J
K
C
U
T
N
S
Q
B
A
II
I

Figure 11. Kinosternon leucostomum males, plots of population means on first (I) vs. second (II) canonical variates (data standardized with ratios).

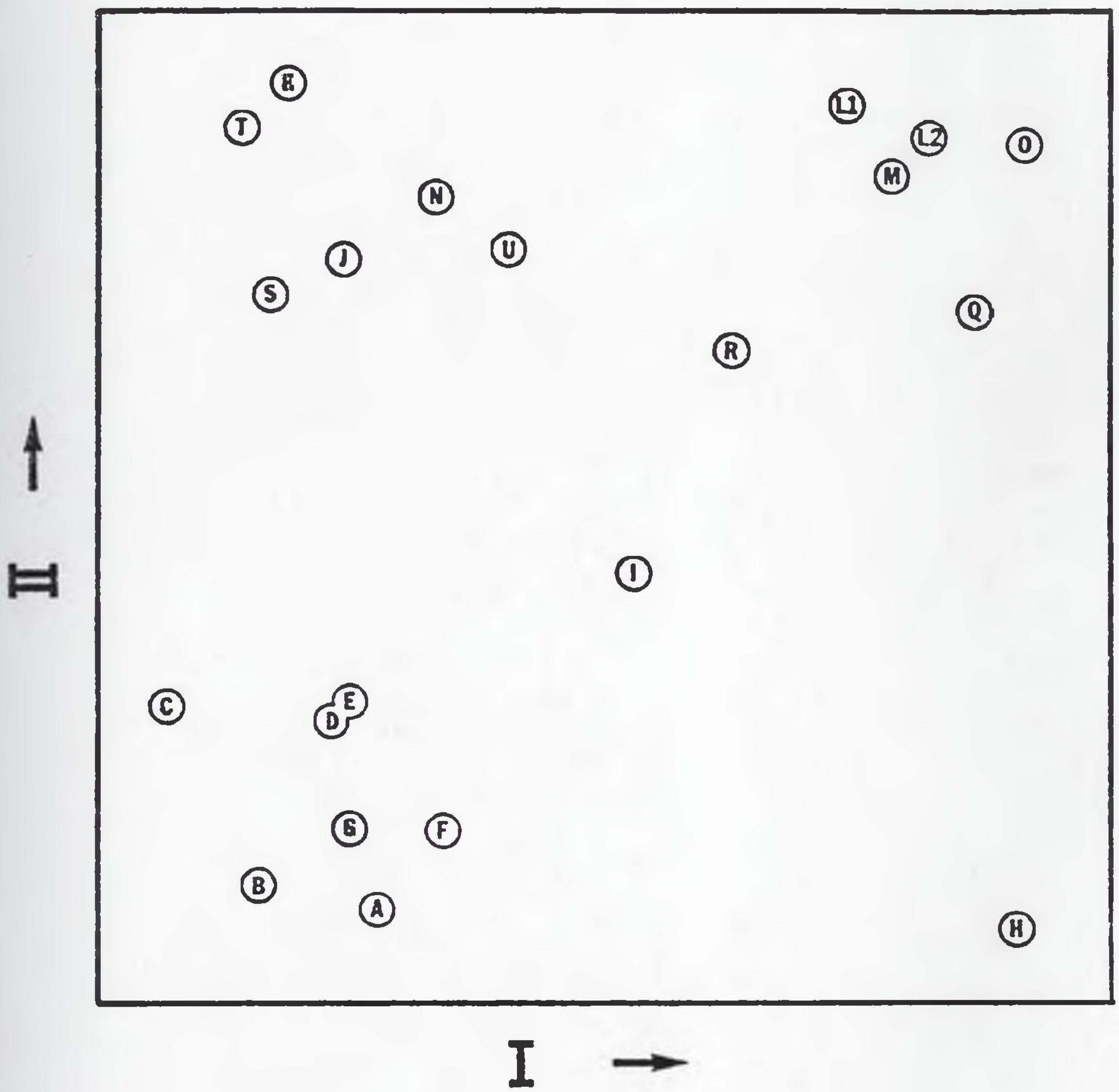
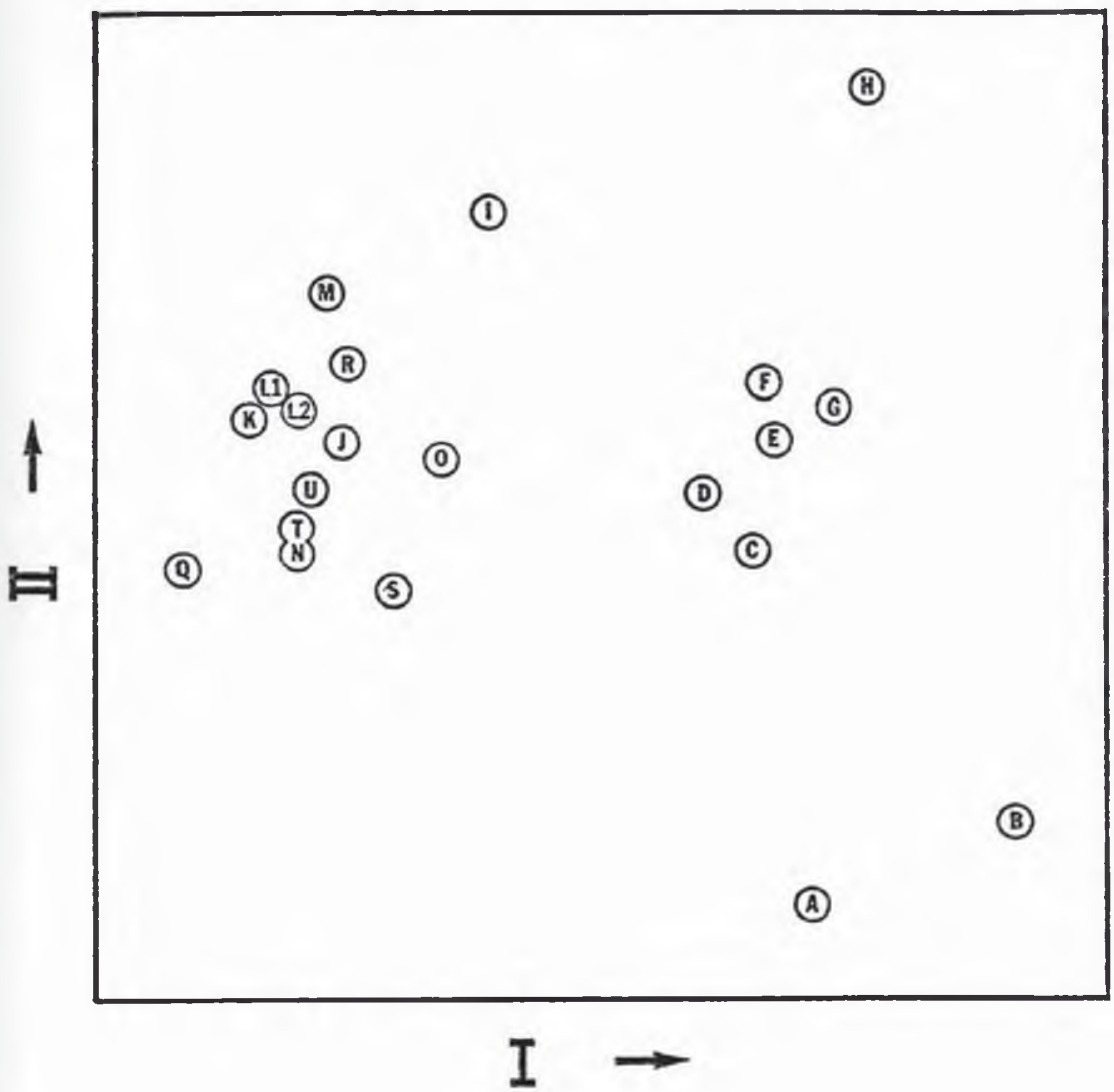

K
T
L1
L2
O
M
N
U
J
S
Q
R
II
I
C
E
D
G
F
B
A
H
I

Figure 12. *Kinosternon leucostomum* females, plots of population means on first (I) *vs*. second (II) canonical variates (data standardized with ratios).


H
I
M
R
L1
L2
K
J
O
U
T
N
Q
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F
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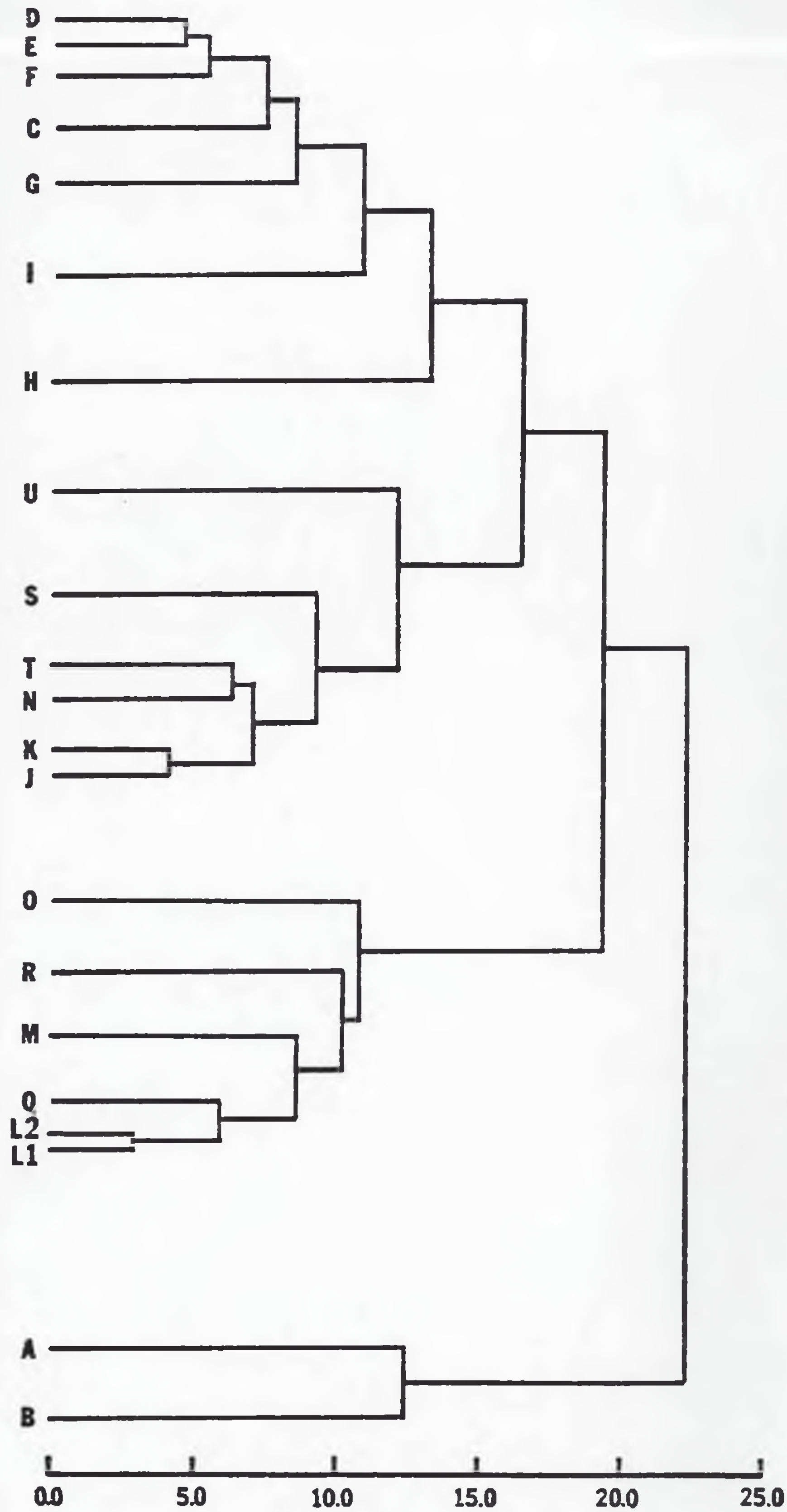
C
B
A
II
I

Figure 13. Kinosternon leucostomum males, dendrograph of D^2 values (data standardized by regression).


D
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F
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M
Q
L2
L1
A
B
0.0
5.0
10.0
15.0
20.0
25.0

Figure 14. Kinosternon leucostomum females, dendrograph of D^2 values (data standardized by regression).

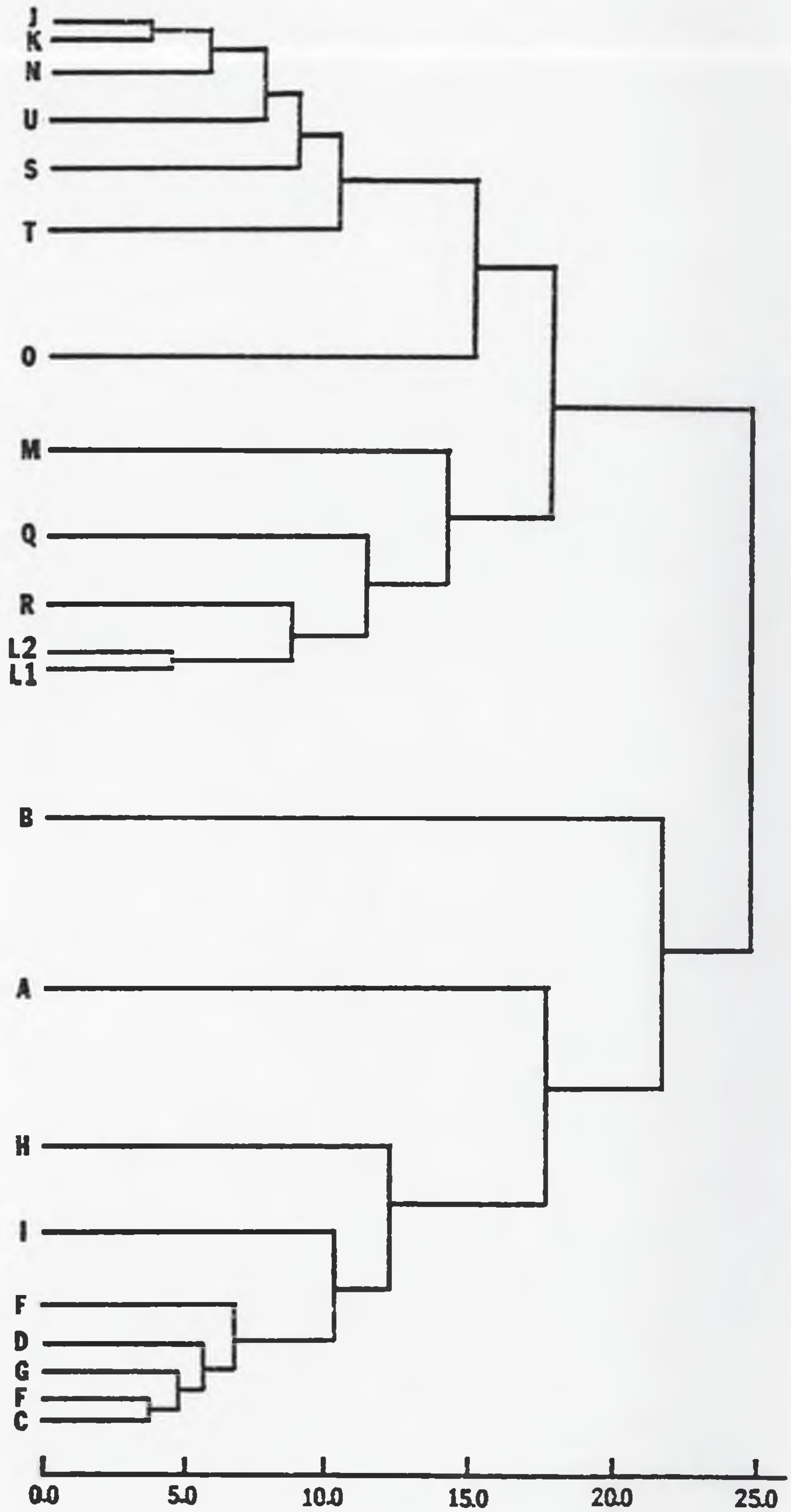

J
K
N
U
S
T
O
M
Q
R
L2
L1
B
A
H
I
F
D
G
F
C
0.0
5.0
10.0
15.0
20.0
25.0

Figure 15. Kinosternon leucostomum males, dendrograph of D^2 values (data standardized with ratios).

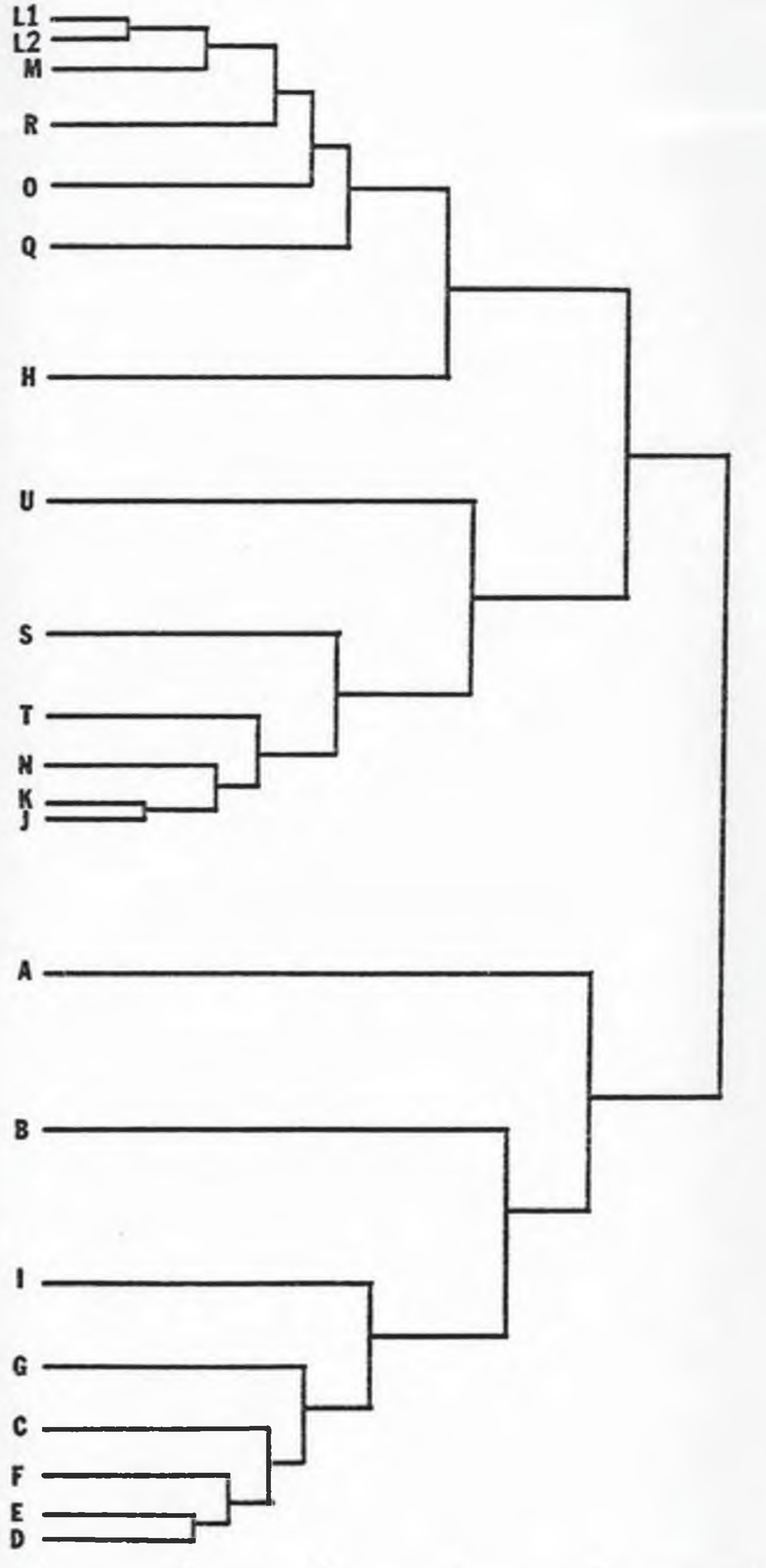
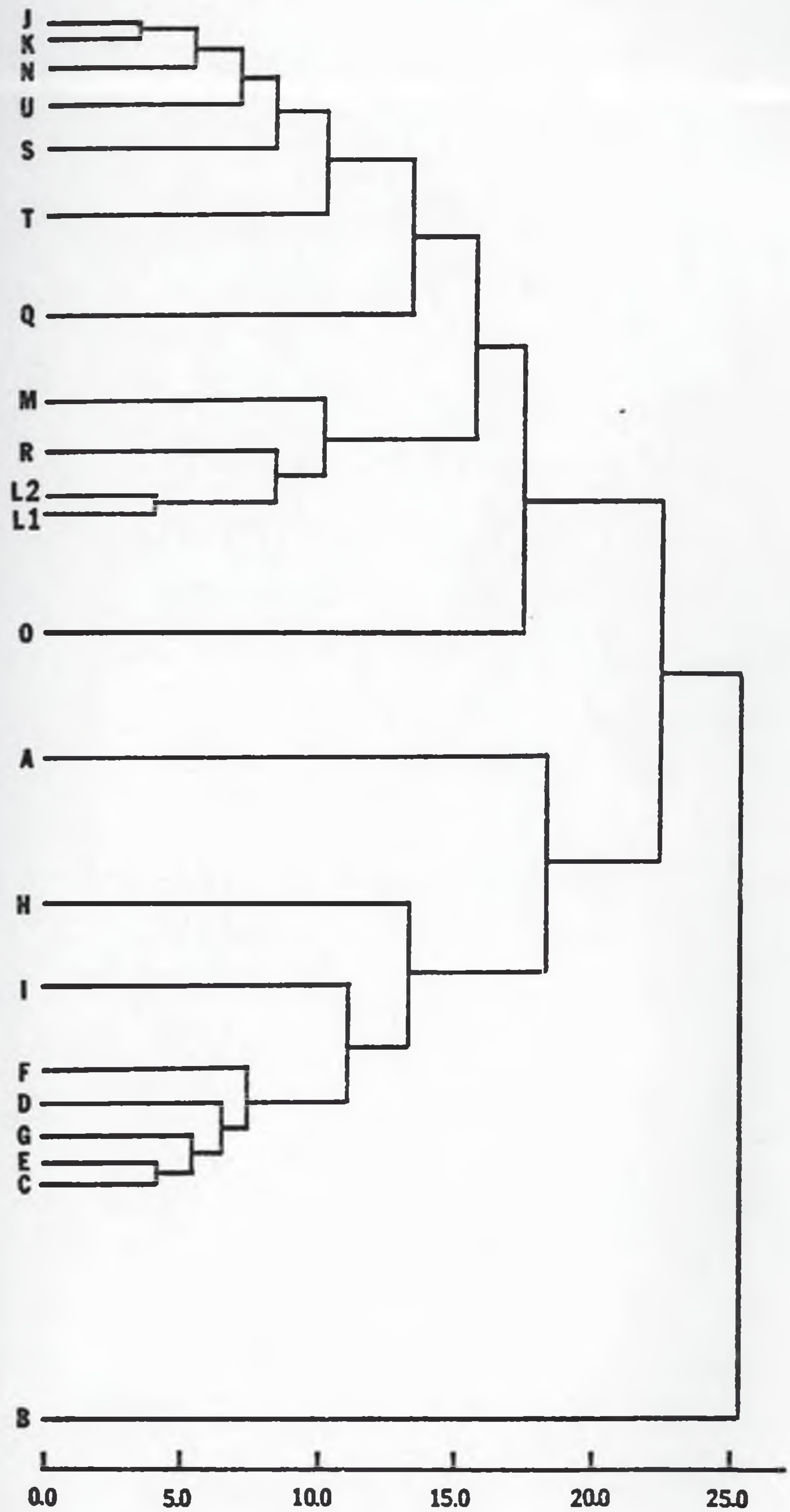

L1
L2
M
R
O
Q
H
U
S
T
N
K
J
A
B
I
G
C
F
E
D
0.0
5.0
10.0
15.0
20.0
25.0

Figure 16. Kinosternon leucostomum females, dendrograph of D^2 values (data standardized with ratios).


J
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L2
L1
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B
0.0
5.0
10.0
15.0
20.0
25.0

section.

Based on the above comparisons, it seems reasonable to conclude that the complications resulting from the use of ratios as input variables in these multivariate analyses are not nearly as serious as might be suggested on theoretical grounds (Atchley et al., 1976). The results of the multivariate analyses used in this study are used as descriptive tools only; no statistical significance is associated with them. Interpretations of these results are based on visual representation of (1) phenetic similarities among groups and individuals, and (2) relative importance of characters in explaining phenetic patterns, and are subject to the limitations of all such analytical techniques regardless of the methods used for data standardization (Sneath and Sokal, 1973, p. 31 ff.). Since generating size corrected variables by any technique other than ratios is complex and expensive and yields less useful results in general, the present study is based on results from analyses using ratios as input variables.

Results of Multiple Discriminant Analyses

An analysis of the characters added to the discriminant equations at each step (from the summary tables) allows a determination of those characters, in order, which contribute most heavily to the patterns of variation observed. Furthermore, since the MDA determines characters which are significantly correlated with those added first to the discriminant equation, it is possible to identify "character complexes", or sets of highly intercorrelated characters which tend to be frequently associated with each other and are possibly inherited as a group.

The results of the discriminant analyses are presented as follows for K. leucostomum, K. integrum, and K. scorpioides respectively: mean value of each character for each population in Tables 15-16, 19-20, and 29-30; standard deviations of each character for each population in Tables 17-18, 21-22, and 31-32; within groups correlation coefficients in Tables 5-6, 23-24, and 33-34; numbers of specimens assigned to each group by MDA in Tables 9-10, 25-26, and 35-36; summary tables of MDA analyses in Tables 13-14, 27-28, and 37-38.

These results are discussed separately for males and females of K. integrum, K. scorpioides, and K. leucostomum. The first eight to eleven characters selected (i.e., those with the highest information content), their correlations to other characters, and (when possible) their functional and evolutionary significance are discussed below in the order they were selected by the discriminant analyses.

Kinosternon integrum Analyses

Males

1. M11 (is M10 higher than M11?). There is significant correlation with M11 and no other characters (Table 23). Since juveniles of most Kinosternon differ from adults in having M10 and M11 roughly the same height (cf. Conant and Berry, 1978), it is possible that this character is an ontogenetic one. Those populations in which M10 is least frequently lower than M11 are 3 and 4 (central Pacific Coast), 8B (coastal Jalisco), and 12 (Río Tamesí).

2. DKL (degree of lateral keeling). There is significant correlation with character DKC only; i.e., the lateral and central keels tend to vary as a unit. The distributional pattern of DKL suggests that male *K. integrum* from the lower Río Balsas, southern Pacific Coast, and Gulf of Mexico drainages have on average more prominent carapacal keels ($\bar{X} > 1.10$) than most populations from the northern and central Pacific Coast, or the Plateau of Mexico (Table 19).

3. INL (length of the inguinal scute). INL forms a highly intercorrelated character complex with the following: CWA, CWP, ABL, AHW, PHW, TFW, SHT, BRL, C1L, C1A, C3L, and HPW. That is, there is a tendency for populations with relatively long inguinal scutes also to have relatively wide, highly domed shells, relatively long central scutes, and extensive plastrons (i.e., those with sufficient ventral surface area to occlude the ventral openings of the shell) with long abdominal scutes. Those populations with the shortest inguinals (and flattest, narrowest shells with small plastrons) are those along the southern Pacific Coast (populations 6, 8B, 10, 14-17, and 20B). However, the population with the shortest inguinal of all is 1A, which has a flat, narrow shell, but an extensive plastron (large ABL, AHW, PHW, TFW, and BRL).

4,6-8. BRL (bridge length), AHW (anterior hinge width), CWA (carapace width anterior), and PHW (posterior hinge width). These are all part of the character complex described above. It is possible to delineate more clearly the characters involved in the complex by examining significant intercorrelations from Table 23. The following characters are involved: CWA, AHW, PHW, TFW, SHT, BRL, C1L, C1A, C3L, C3W, INL, HPW, FAW, and GUW. The evolutionary and ecological significance of this character complex will be discussed under "Evolution of Plastron Size."

5. AXL (axillary scute length). AXL is statistically significantly correlated with nothing else. In general, axillary scutes are longest in populations from the mid-southern Pacific Coast (10, 14-16). Since these populations are also some of those with the smallest bridges and plastrons (see above), it seems likely that the presence of a large axillary scute may serve to strengthen mechanically the anterior bridge area.

9. GUL (gular scute length). The longest gulars are found in *K. alamosae* (population 1A) and many Mexican Plateau populations 9A, 9B, 11B, 17-19; i.e., the Río Lerma, and Upper Río Balsas. The smallest are in populations 1B, 4,5, 8B, 12, 15, 16, and 20B, or much of the Pacific Coast.

The remaining characters added to the discriminant analysis which contribute significantly to the discriminant equation are all members of the character complex described above.

Females

1. AHW (anterior hinge width). AHW is significantly correlated with CWA, CWP, PHW, TFW, ANL, BRL, and HPW. This suggests a pattern in which broad carapaces and extensive plastrons are associated, a pattern nearly the same as that for males. Anterior hinge width is greatest in *K. alamosae* (population 1A), and, in general, in populations on the Mexican Plateau irrespective of drainage basin (7, 9A, 9B, 11A, 12, 17, 19, 20A). It is smallest (i.e., the plastron is

narrowest) in central and southern Pacific Coast populations (4-6, 8A, 8B, 10, 14-16), although it is clear that individuals from groups 8B (coastal Jalisco) and 20B (K. oaxacae) have much smaller plastrons than any other close relatives of integrum.

2. ABL (abdominal seam length). ABL is significantly correlated with BRL (i.e., as abdominal scute length increases, the bridge becomes larger). The population with the proportionately longest ABL is 1A (K. alamosae); the populations with the smallest ABL are 8B (coastal Jalisco) and 20B (K. oaxacae). In general, ABL is largest in populations from the mid and southern Pacific Coast, while the longest are in northern Pacific Coast and Plateau populations.

3. AXL (axillary scute length). AXL is significantly correlated with AIC only; i.e., those animals with larger axillary scutes tend to have a greater probability of axillary-inguinal contact. AXL is smallest in K. alamosae (1A), and is largest in 11A, 12, 14, 16, and 20A (central Mexican Plateau, Río Tamesí, and southern Pacific coast.

4. DKL (degree of lateral keeling). As in males, DKL is significantly correlated with DKC only. DKL is least in K. alamosae and is greatest in K. oaxacae. Distributional patterns are not clear, but it appears that north and central Pacific Coast populations, as well as some Mexican Plateau populations have the least keeling, while southern Pacific Coast and some Mexican Plateau populations have most.

5. SHT (shell height). SHT is significantly correlated with PHW, TFW, and BRL. This is the first suggestion that the character

complex identified in males of _integrum_ may also be evident in females. It is clear, at least, that higher shells are correlated with wider plastrons and longer bridges. Those populations with the highest shells are _K. alamosae_ (1A), 5-6 (central Pacific Coast), 9B, 12, 19 (Mexican Plateau), and 20B (Río Verde); those with the shallowest shells are 8B, 14-15, and 20B (southern Pacific Coast). These patterns are reminiscent of, but by no means identical to, those for males.

6-7. _M11_ (is M10 higher than M11?) and _M2C_ (does C1 contact M2?). The functional and evolutionary significance of these is not clear, but may be ontogenetic. M11 is least in northern Pacific Coast populations (1B, 2-4) and some scattered Mexican Plateau populations (9A, 12, 18-19). M2C is far lowest in populations 1A (_alamosae_) and 8B (coastal Jalisco), but is also small in populations 2, 5, 10, 11A, 16 and 20B.

8. _INL_ (inguinal scute length). INL has no statistically significant correlations to other characters. Long inguinals are found in mid-Pacific Coast and some Mexican Plateau populations, while the shortest are in 1A (_alamosae_), 20B (_oaxacae_), and 8B (coastal Jalisco).

9. _ANL_ (anal seam length). It is significantly correlated with AHW, PHW, TFW, FEL, and BRL, and is clearly part of the recurrent character complex noted above. That ANL should be so highly negatively correlated with FEL is unsurprising. Since females possess on average a much less emarginate anal notch (NOT), as interanal seam length (ANL) increases, it must be primarily at the expense of a

shorter interfemoral seam (FEL). The smallest ANL's occur in populations 8B and 20B, although they are also small in all mid and southern Pacific Coast populations. The largest interanal seams are in northern Pacific Coast, western Mexican Plateau, and Río Balsas populations of integrum.

10-11. C3W and C1L. Unlike the male analysis, these show no significant correlations to other characters. Patterns are difficult to detect, but there is a tendency for northern Pacific and Mexican Plateau populations to possess narrow third centrals, and long first centrals.

Remaining characters of significance are BRL, PHW, HUL, PEL, FEL, AIC, and GUL, all of which appear to be associated with the recurrent character complex either by high correlation coefficients, or by similar distributional patterns.

Kinosternon scorpioides Analyses

Males

1. ANL (anal seam length). ANL has significant negative correlation with FEL. As interanal seam length increases, femoral length decreases. Furthermore, interanal length is longer when NOT is least; i.e., when the anal notch is least emarginate. Both of these factors are in effect (ANL is least, but NOT and FEL are large) in populations 39-40 and 45-54, or southern Pacific Coastal Central America and South America. ANL is largest (FEL and NOT are smallest) in Yucatán (Atlantic) and El Salvador (Pacific).

2. AIC (are axillary and inguinal scutes in contact?). AIC is

significantly correlated with nothing else. Mexican populations have the least inguinal-axillary contact. Beginning with populations 32 (El Salvador, Pacific), and 42 (Nicaraguan Caribbean Coast) and proceeding southeast, the frequency of inguinal-axillary scute contact increases. Southern Central American, and all South American populations have frequent contact. Broad contact between axillary and inguinal scutes tends to be associated with narrow bridges (BRL) and small plastrons, suggesting that wide inframarginal scutes may help structurally to strengthen the bridge area when it is unusually small.

3. ABL (abdominal scute length). ABL has a high though not statistically significant correlation with BRL. ABL is largest in Mexican (including Yucatán) populations, Caribbean Nicaragua, and Argentina. It is intermediate in some northern Central Pacific (32, 35-38) populations, as well as northern South America. ABL is smallest in some northern and some southern Central American populations (49-53).

4-5. PHW (posterior hinge width) and CWP (carapace width, posterior). PHW and CWP are significantly correlated to each other as well as to a number of other characters which would suggest the presence of a highly intercorrelated character complex as seen in *K. integrum*. It appears that the following characters are involved: CWA, CWP, AHW, PHW, TFW, HUL, ANL, SHT, BRL, HW, C1L, and C3W. Extensive plastrons are correlated with wide, high shells, long bridges, and (to a lesser extent) wide heads. In general, the widest, highest shells, most extensive plastrons, and longest bridges are in extra-Yucatecan México, northern and southern Central America (Pacific and Caribbean), and Argentina; they are slightly smaller in Yucatecan and northern Panamanian populations. Southern Panamanian (39-40, 45) and South American populations (except Argentina) have much narrower, flatter shells, smaller plastrons, and shorter bridges.

6. BRL (bridge length). It is most highly correlated with (though not with statistical significance) with CWA, ABL, AHW, and PHW; i.e., it has an association with the above character complex. The longest bridges are found in populations from México, Belize, the northern Mosquito Coast of Nicaragua, and Argentina. The shortest bridges are found in Panamanian and South American populations, while those in mid-Pacific Central America are intermediate.

7. C1L (first central scute length). While it is significantly correlated only with C5L, C1L has high positive correlation with CWA, CWP, AHW, PHW, C1A, and C5W suggesting it, too, is part of the character complex noted above.

8. HW (head width). HW has statistically significant correlation with no other characters, but has greatest correlation with characters involved in the character complex above. The widest heads are in populations on the Guatemalan Plateau and Belize (26, 31), southern Central America (39), and northern South America (52,53); while the smallest heads are in the population from the Río Grande de Chiapas (24), and northern South America (50, 54). I have shown elsewhere that head width is a function of the degree to which mollusk-crushing morphology is present in *Sternotherus* (Berry, 1975). During the course of the present study, I examined the gut contents

of six adult *K. scorpioides* (three males and three females) from a population in which megacephally is evident (population 31, Belize; HW = .221 of CL), and six *K. scorpioides* from a nearby population with small heads (population 28, Yucatán; HW = .186 of CL). The guts of the megacephalic specimens all contained fragments of unidentified hard-shelled gastropods; none of the guts from the small-headed specimens contained gastropod fragments, although four of six contained measurable quantities of food. The presence of megacephally in *K. scorpioides* appears to be a dietary specialization.

9. C3W (third central scute width). C3W has high but not statistically significant correlation with CWA, CWP, PHW, SHT, and HW, suggesting it, too, is associated with the character complex described above.

Females

1. AIC (are axillary and inguinal scutes in contact?). AIC has no significant correlations to other characters. As in the analysis of males, axillary-inguinal contact is least in Mexican and northern Central American populations, intermediate in central Central America and Argentina, and greatest in southern Central America and South America.

2. TFW (trans-femoral plastral width). TFW has statistically significant correlation with CWA, CWP, AHW, PHW, and SHT, and high though not statistically significant correlation with ANL, BRL, and HW. Female *K. scorpioides* exhibit a highly intercorrelated character complex similar to that in male *scorpioides*, and all *K. integrum*; i.e., animals with extensive plastrons tend also to have wide, high

carapaces. TFW is widest in mid-Pacific Central America, slightly less in México, Caribbean Nicaragua, and Costa Rica. It is least in northern South America and adjacent Panamá.

3. ABL (abdominal seam length). It is significantly correlated with BRL, i.e., animals with a long fixed portion of the plastron tend to possess correspondingly long bridges. ABL is least in northern Central American Pacific Coast (25, 32-33) and Argentinian (54) populations. It is largest in populations along the Atlantic versant of southern México and Guatemala, middle Central America (Caribbean and Pacific), and two South American populations (47, 53). The lack of correlation between ABL and the recurrent character complex noted above is surprising. Apparently, an extensive plastron, and wide, high shell can be associated with either a very long (24, 35, and 42) or a very short (25, 32, and 33) fixed portion of the plastron. The functional significance of this situation is not clear.

4. HW (head width). HW is significantly correlated with SHT, and highly correlated with CWA, PHW, TFW, and ClP. As in males, HW seems to be associated with the character complex above. HW is greatest in Belize (31), southern Central America (44-45), and one South American population (53); it is smallest in the Río Grande de Chiapas (24), Yucatan Peninsula (28-30), and Argentina (54). As in males, this pattern is likely the result of local ecology and dietary habits. The fact that the patterns of distribution of HW were slightly different in females than in males suggests that sexual dimorphism in this character is greater in some populations than in others.

5. BRL (bridge length). BRL is significantly correlated with ABL only. Female scorpioides with the longest bridges occur in southern México and the Yucatán Peninsula, while the shortest bridges are in mid and southern Central American populations.

6-7. ANL (anal scute Length) and FEL (femoral scute length). ANL and FEL are negatively correlated with each other (as in males). ANL is significantly correlated with CWA, CWP, AHW, TFW, and SHT (FEL has high though not significant negative correlations with these) suggesting that these characters are associated with the same character complex as above. ANL is largest in México (excluding Yucatán), northern and central Pacific Central America; while it is smallest in South America excepting Argentina.

8. C1L (first central scute length). C1L has no significant correlations to other such characters, but has high positive correlations to AHW and C1A, and large negative correlations to C5L and C5W. That is, a relatively long first central scute is associated with a wide anterior hinge and wide first central scute; but as the length of C1 increases, the length and width of C5 decreases. Patterns of variation in this character are difficult to determine, but it appears C1 is proportionately largest in northern and mid Central American, one northern South American, and the Argentinian populations. It is shortest in the Río Grande de Chiapas, Cozumel, southern Central America, and most northern South American populations.

9. DKL (degree of lateral keeling). DKL is significantly correlated with DKC. The greatest keeling is present in populations from Yucatán (29-31) and South America including Argentina (48-54); while

it is least in northern and mid Pacific Central America (35-38).

10-11. SHT (shell height) and CWA (carapace width, anterior). Both SHT and CWA are part of the recurrent character complex outlined above. Shell height is greatest in female *scorpioides* from Mexico (including western Yucatán) (21-23, 28-30), Belize (31), the vicinity of Lake Nicaragua (35), and San Andres Island, Colombia (44); while shells are shallowest in South America excluding Argentina (47-52), and in the Río Grande de Chiapas (24). The widest shells anteriorly are in México excluding the Yucatan Peninsula (21-23, 25), and the Pacific Coast of northern and mid Central America (32-34); the smallest CWA are in northern South America and southern Central America (45-54), the Mosquito Coast of Nicaragua (43), the Río Grande de Chiapas (24), and the northeastern tip of the Yucatan Peninsula (29).

Kinosternon leucostomum Analyses

Males

1. TFW (trans-femoral width of plastron). TFW is significantly correlated with CWA, CWP, AHW, PHW, and FAW, and appears to represent an intercorrelated character complex similar in form to those identified in *K. integrum* and *K. scorpioides*; that is, there is a general tendency for populations with extensive plastrons to have wide, high shells and large heads. Populations of *leucostomum* from México, the Caribbean Lowlands of southern Nicaragua and Costa Rica (population J), and South America have large TFW; while populations from southern Central America (southern Costa Rica and Panamá; populations L, L2,

M, O, Q, and R), and the southern Nicaraguan Mosquito Coast (H, I) have the smallest.

2-3. SHT (shell height) and ABL (abdominal scute length). SHT has no significant correlation to other characters. Populations from México and Guatemalan Plateau drainages have the highest shells; while those from the southern Mosquito Coast (H, I), Pacific Costa Rica and Panamá (L, L2, M, O) have the flattest. The third character, ABL, likewise has no significant correlations. Mexican and northern Central American populations have the shortest interabdominal seams, while southern Central American populations have the longest.

4. CWP (carapace width, posterior). It is significantly correlated with CWA, PHW, and TFW, and is a part of the character complex noted above. CWP is largest in populations from Mexican drainages north of the Río Grijalva, southern Central America, and South America; it is largest in populations inhabiting the Atlantic versant of northern Central America as far south as Nicaragua and the Mosquito Coast.

5. GUL (gular scute length). GUL has a significant negative correlation with HUL (i.e., as the length of the gular scute increases, interhumeral seam length decreases). GUL is largest in populations inhabiting Atlantic drainages from the Mosquito Coast northward.

6. INL (inguinal scute length). INL is significantly correlated with no other characters. Inguinal scutes are longest in populations from Guatemalan Plateau drainages (C, D), and in western South America (S, T); and shortest in populations inhabiting Caribbean drainages from the Mosquito Lowlands south, and the

Colombian Río Magdalena (U).

7. PHW (posterior hinge width). PHW is also part of the character complex above, being significantly correlated with CWA, CWP, AHW, and TFW. PHW is largest in Atlantic populations north of the Mosquito Lowlands and South America; while it is smallest in all Central American systems from the Mosquito Lowlands southward.

8. ANL (anal seam length). ANL has no significant correlations to other characters, but its highest correlations are with AHW and TFW suggesting an association with the recurrent character complex. A high negative correlation with FEL suggests that as interanal seam length increases, interfemoral length decreases (the same pattern as seen in *integrum* and *scorpioides*). ANL is largest in Mexican and Central American populations as far south as the northern Mosquito Lowlands of Nicaragua, and smallest in southern Central American populations (L, L2, M, O, Q, and R).

Females

1. SHT (shell height). SHT has significant correlations with no other characters, but highest correlations with TFW, ANL, and HW. Populations with the highest shells are those in drainages of the Guatemalan Plateau northward (A-D), the Osa Peninsula of Pacific Costa Rica (O), and northwestern Colombia. The flattest shells occur in those populations in the southern Mosquito Lowlands.

2. ABL (abdominal seam length). ABL has no significant correlations with other characters but a high correlation with BRL. Interabdominal seam lengths are longest in southern Central American and South American populations; and shortest in populations from Atlantic

drainages from the Mosquito Lowlands northward.

3-4. C1L (first central scute length) and INL (inguinal length). Neither C1L nor INL is significantly correlated with other characters. C1L is longest in northern Gulf of Mexico (A, B) and Goofy Lake, Panamá (Q) populations, and shortest in most middle and southern Central American populations. Inguinal scutes are longest in South American and Mexican populations, and shortest in Mosquito Lowlands populations.

5-7. AHW (anterior hinge width), CWA (carapace width, anterior), and PHW (posterior hinge width). They are significantly correlated with each other, and with CWP, TFW, and HPW. That is, they are all three part of the character complex described above. AHW is largest in Mexican populations, smallest in populations from the southern Nicaraguan Mosquito Lowlands (H, I) and southern Central America, (L, L2, M, O, R). CWA is largest in Gulf of Mexico drainages (A-C), and some populations in eastern Panama (Q-R); and smallest in Central American populations below Lake Nicaragua (Caribbean and Pacific, J-K, N), and northwestern Colombia (S). PHW is largest in Atlantic drainages of the Guatemalan Plateau northward (A-E), and Pacific Central America below Lake Nicaragua (N-O); and smallest in Mosquito Lowlands (F-I) and San Blas, Panamá (M) populations.

8. HW (head width). HW is significantly correlated with no other characters, but which has highest correlations with CWA, CWP, AHW, PHW, and SHT suggesting a relationship with the character complex above. Head widths are generally greatest in Mexican populations (A-C), and least in populations from Central America below Lake Nicaragua

(K-N). Adult males from population B have the largest heads (HW = .213 of CL), but there is never an indication of the development of megacephally as was shown for *K. scorpioides*.

Phenetic Relationships Among Populations

Since the first two canonical variates account for 50-52% (*K. integrum*), 58-62% (*K. scorpioides*), and 57-58% (*K. leucostomum*) of the dispersion represented by all axes generated, a comparison of mean values for each population on the first two canonical variates provides a good representation of phenetic relationships among populations.

Dendrographs of distance measures (D^2) present all information available in the system, although as a method of presentation their dimensionality is limited, and there is frequently considerable distortion (see Sneath and Sokal, 1973).

It is hoped that an accurate picture of phenetic relationships among populations can be had by utilizing the results of both types of analysis.

Kinosternon integrum Analyses

Plots of the first *vs*. the second canonical axes are presented in Fig. 17 for males and Fig. 18 for females of *K. integrum*. Dendrographs of *K. integrum* based on D^2 values are presented in Fig. 19 for males and Fig. 20 for females.

Males

Examination of Fig. 17 reveals that groups 20B and 1A are greatly dispersed along the first and second axis respectively. The rest of the populations form a comparatively compact and homogeneous cluster; North Pacific Coast and Mexican Plateau populations tend to cluster together, and to form a continuous cluster with southern Pacific Coast populations. Southern Pacific Coast populations are closest to but discrete from population 20B.

Examination of the dendrograph in Fig. 19 generally supports the above. Group 20B is extremely distinct, as are 1A and 8B. The rest of the populations form a tight cluster, but southern Pacific Coast *integrum* are clearly more similar to each other than to the other groups. It is noteworthy that specimens from the lower Río Balsas (15) cluster without question with the other populations along the southern Pacific coast, while those from the middle and upper Balsas basin (17-18) cluster equally clearly with Mexican Plateau populations.

Females

From examination of Fig. 18 it is clear that group 1A is distinctively separate from the rest of the *integrum* cluster along the first canonical axis. Group 20B is separated along the second axis, but, in this case, group 16 (southern Pacific Coast) is intermediate between 20B and the rest of the cluster. All southern Pacific Coast populations are grouped together and are more-or-less continuous with the *integrum* Plateau and northern Pacific Coast populations, but less so than in the analysis of males above.

The dendrograph in Fig. 20 indicates that *K. integrum* females have phenetic relationships generally similar to those for males, in that populations 20B, 8B, and 1A are quite discrete from the bulk of the *K. integrum* cluster at distances of 28.8 to 21.4, although the order differs with respect to 1A and 8B. Southern Pacific Coast relationships to the rest of the *integrum* populations are less obvious. Populations 20A and 16 are distinct at distances of 18.5 and 15.5 respectively; populations 14-15 are closer to each other than to any other population, but they are, in turn, more similar to the bulk of the Mexican Plateau-northern Pacific Coast cluster than to southern Pacific Coast populations (distances of 12.0 and 15.5 respectively). Population 10 (Ríos Coahuayana and Armería) is more similar (9.1) to some Mexican Plateau populations than the nearest (geographically) Pacific Coast populations.

In summary, the following generalizations can be made regarding the phenetic relationships of *Kinosternon integrum* and its closest relatives: (1) population 1A (*K. alamosae*) is consistently phenetically distinct from all other populations; (2) population 20B (*K. oaxacae*) is distinctly different from other populations on the basis of the dendrographs in Figs. 19 and 20, although examination of canonical axes (Figs. 17 and 18) suggests it is considerably more similar to populations from the southern Pacific Coast (14, 15, and 16 in particular) than to any others; (3) southern Pacific Coast populations are more similar phenetically to each other than to northern Pacific Coast or Mexican Plateau populations. The lower Río Balsas population (15) is most similar to other southern Pacific Coast populations; the upper Río Balsas population (18) has greatest affinities to Mexican Plateau populations, while the middle Río Balsas population (17) is intermediate (the possibility exists that the intermediacy is due to the presence in the sample of individuals from both areas to the north and south rather than a truly intermediate population, since Tables 25 and 26 indicate that many specimens originally assigned to group 17 in the discriminant analysis were classified with either Plateau or lower Balsas populations). The remainder of *K. integrum* populations are remarkably phenetically homogeneous, showing none of the sorts of consistent phenetic clustering mentioned above.

Kinosternon scorpioides Analyses

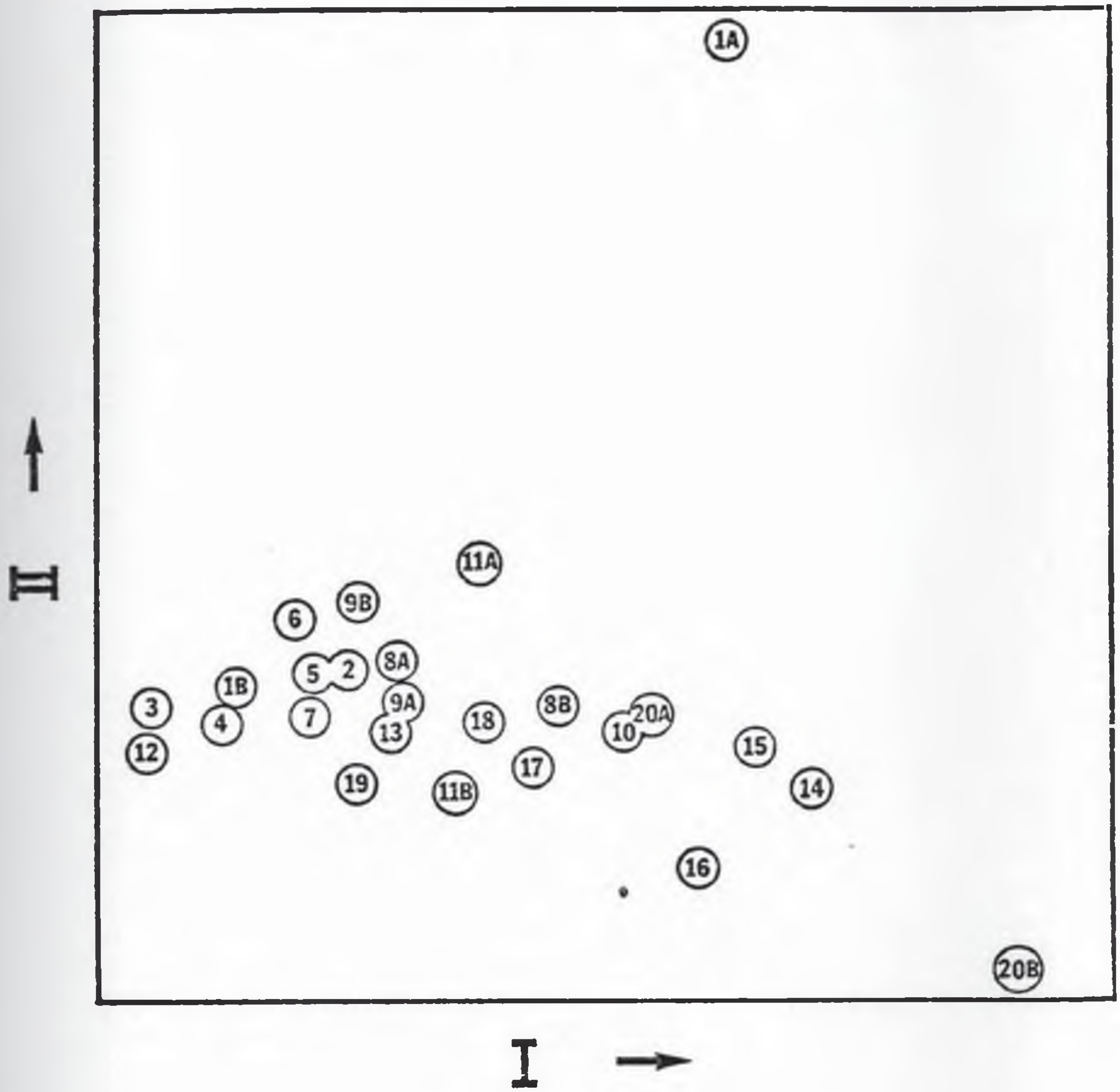
Plots of the first *vs*. second canonical axes are presented in Fig. 21 for males, and Fig. 22 for females of *Kinosternon scorpioides*. Dendrographs of *K. scorpioides* populations based on distance values (D^2) are presented in Fig. 23 for males, and Fig. 24 for females.

Males

Examination of Fig. 21 indicates that Mexican and Central American populations are separated from South American populations with groups 38-39 and 51 intermediate (eastern Panamá and eastern Brazil). Population 54 (Argentina) is noticeably dispersed from the rest of the South American cluster. Along the second axis Mexican, Belize, and Guatemalan populations (21-31) are widely separated from Central American populations (34-37, 42-44), with populations 32-33 (Soconusco Coast) and to a lesser extent 24 (Río Grande de Chiapas) are intermediate.

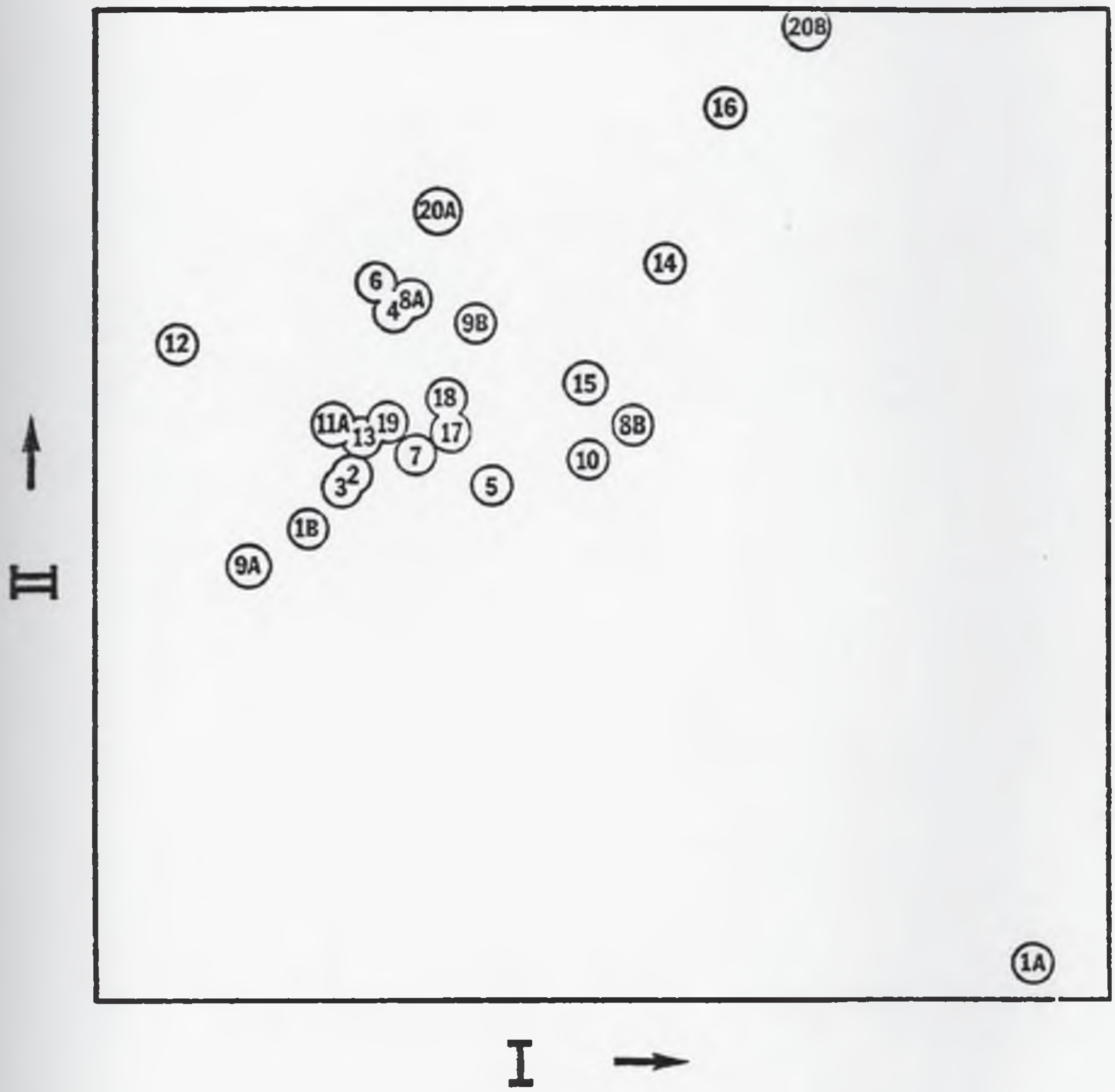
The dendrograph in Fig. 23 generally reinforces these patterns.

Figure 17. *Kinosternon integrum* males, plots of population means on first (I) *vs*. second (II) canonical variates.



1A
11A
9B
6
5
2
8A
1B
3
9A
8B
20A
4
7
13
18
10
15
12
17
14
19
11B
16
20B
II
I

Figure 18. *Kinosternon integrum* females, plots of population means on first (I) *vs*. second (II) canonical variates.



20B
16
20A
14
6
4
8A
9B
12
15
18
11A
19
13
17
8B
7
10
2
3
5
1B
9A
1A
II
I

Figure 19. *Kinosternon integrum* males, dendrograph of D^2 values.

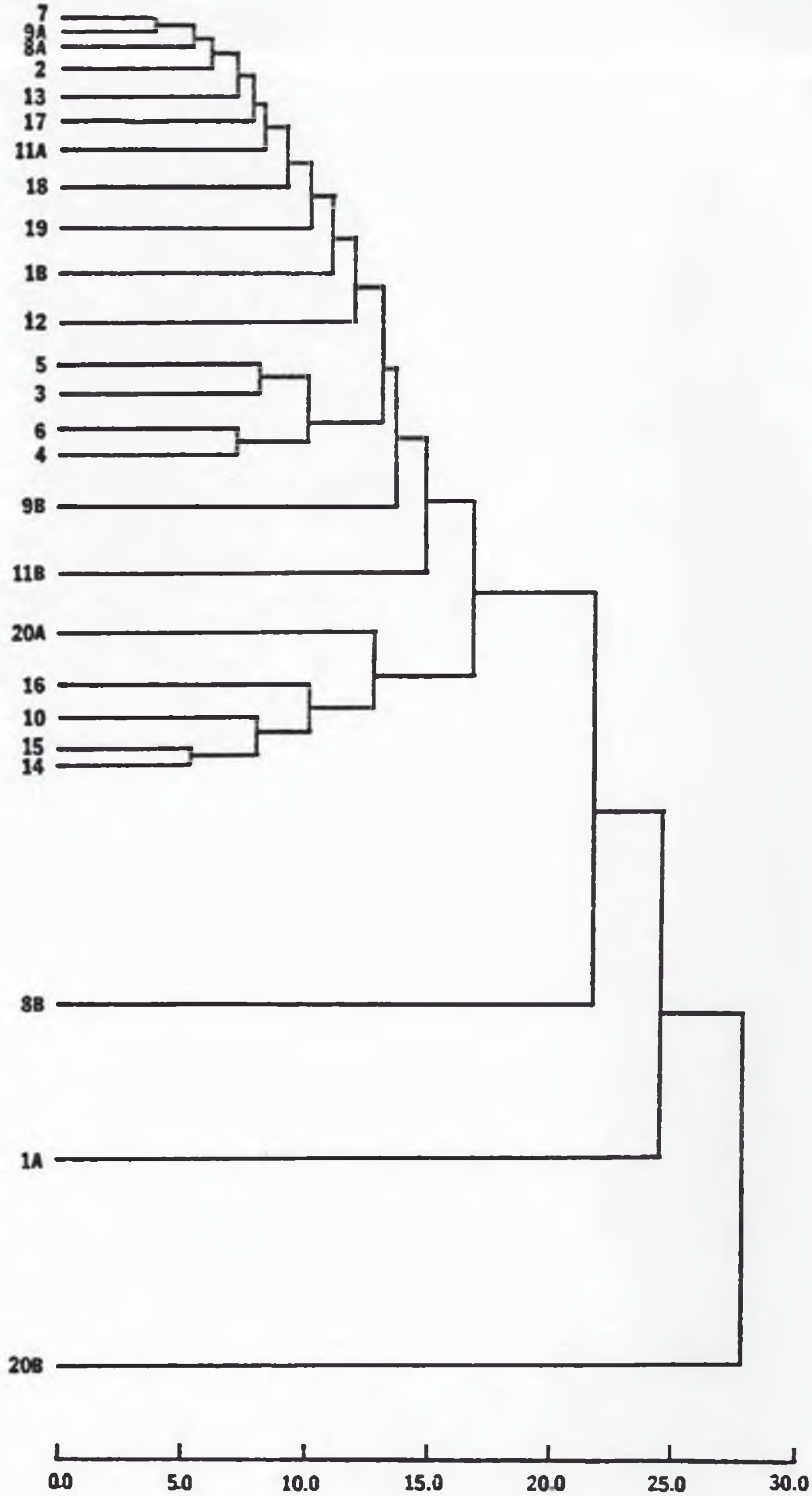
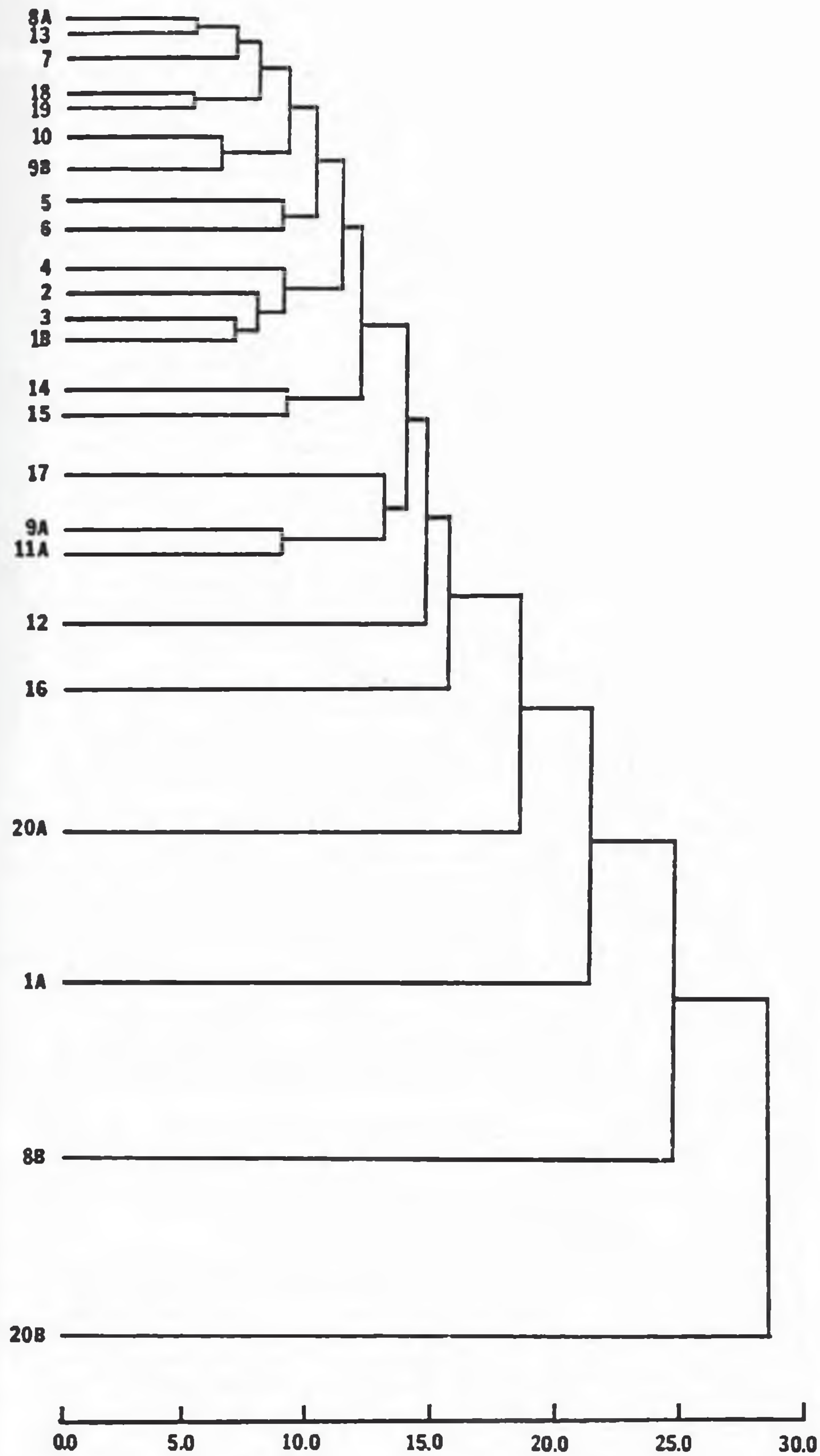

7
9A
8A
2
13
17
11A
18
19
1B
12
5
3
6
4
9B
11B
20A
16
10
15
14
8B
1A
20B
0.0
5.0
10.0
15.0
20.0
25.0
30.0

Figure 20. Kinosternon integrum females, dendrograph of D^2 values.


8A
13
7
18
19
10
9B
5
6
4
2
3
1B
14
15
17
9A
11A
12
16
20A
1A
8B
20B
0.0
5.0
10.0
15.0
20.0
25.0
30.0

There are two general groups of populations: (1) a South American group which contains populations 40, 45-54; and (2) a Central American-Mexican group which includes populations 21-39 and 42-44. The former group is a heterogeneous one which can be divided into two smaller groups; one group containing only population 54 (Argentina), and a second group which contains the other South American populations from which specimens were examined (40, 45-53). The second major group can be easily divided into two distinct subgroups at about the same phenetic level (D^2=22.4 as opposed to 23.6) as in the above case; the two groups consisting of Mexican, Belize, and Guatemalan populations in general (21-31), and the Central American populations (32-39, 42-44). The former subgroup shows three relatively discrete groups of populations within itself; the first of which includes populations 26-27 and 31 (Río Usamacinta and southeastern Yucatán, and Belize), the second (discrete at a level of 14.2) consisting of populations 28-30 (the Yucatan Peninsula), and the third (discrete at 10.2) consisting of 21 (Gulf Coast of México), and 22-23 and 25 (Pacific drainages of the Isthmus of Tehuantepec). Group 24 (Río Grande de Chiapas) is discrete from the bulk of the preceding (16.3), but clusters with Mexican populations in general. The Central American group consists of several phenetically distinct populations (group 39 at a distance of 18.8; group 32 at a distance of 14.5; and group 33 at 11.3), plus the phenetically homogeneous groups containing populations 34, 36-38, and 44 (Central American populations from Golfo Fonseca to the Osa Peninsula, excluding the Nicaraguan Depression, and San Andres Island), and another containing populations 35 and 42-43

(Lago de Nicaragua and the Nicaraguan Depression, and the Nicaraguan Mosquito Lowlands to the immediate north).

Females

From Fig. 22 it is clear that the phenetic relationships among populations of K. scorpioides females is virtually identical with that for males. The first axis effectively separates Mexican, Guatemalan, and Belize populations from Central and South American populations. As above, populations 32-33 (Río Lempa basin) and 24 (Río Grande de Chiapas) are intermediate. Central American populations (34-37, 42-44) are effectively separated from South American populations (40, 45-54) along the second canonical axis.

Phenetic relationships from the dendrographs in Fig. 24 indicate that the relationships are very much as in the analysis of males, although there is considerable reorientation of the clusters. There are two major clusters as above, but this time population 54 (Argentina) clusters more closely with the México-Central American group than to the South American group. In addition, populations 24 (Río Grande de Chiapas) is closer to the Central American groups (32-39, 42-44; at a level of 16.5). Otherwise the two dendrographs are nearly identical with respect to phenetic relationships.

In summary, it is clear that there are three rather discrete and fairly homogeneous groups of populations of Kinosternon scorpioides in this study. The first contains populations 21-23 and 25-31 (i.e., México exclusive of the Río Grande de Chiapas, the Guatemalan Plateau, and Belize. The second group consists of populations 34-37, and 42-44 (Golfo de Fonseca to but not including the Isthmus of Panamá).

Populations 32-33 (El Salvador and the Río Lempa basin) are both geographically and phenetically intermediate. The third group consists of Isthmus of Panamá populations (40, 45), and South American populations (46-53) excepting population 54 (Argentina) which is somewhat discrete. Populations 38-39 (Peninsulas Osa and Azuero), and to a lesser extent 37 (Bahía de Coronada drainages) and 40 (Peninsula de Azuero) to the immediate north and south are geographically as well as phenetically intermediate between the South American-Panamanian group (40, 45, 46-53) and the Central American group (34-37, 42-44). Population 24 (Río Grande de Chiapas) is problematical since it is simultaneously intermediate between the México-Guatemala-Belize group (21-23, 25-31) and the Central American group (34-37, 42-44); but also phentically distinct from either of these groups.

<u>Kinosternon</u> <u>leucostomum</u> Analyses

The first <u>vs</u>. the second canonical axes are plotted in Fig. 11 for males, and Fig. 12 for females of <u>Kinosternon</u> <u>leucostomum</u>. Distance value (D^2) based dendrographs appear in Fig. 15 for males and Fig. 16 for females.

<u>Males</u>

From examination of Fig. 11 it can be seen that Central and South American populations are dispersed, while a group including populations L, L2, M, O, and Q is separated from Central American populations immediately to the geographic north (J, K, N) and to the south in South America (S, T, U). Populations J, K, N and S, T, U tend to cluster together, but are separated from the first mentioned group.

Figure 21. Kinosternon scorpioides males, plots of population means on first (I) vs. second (II) canonical variates.

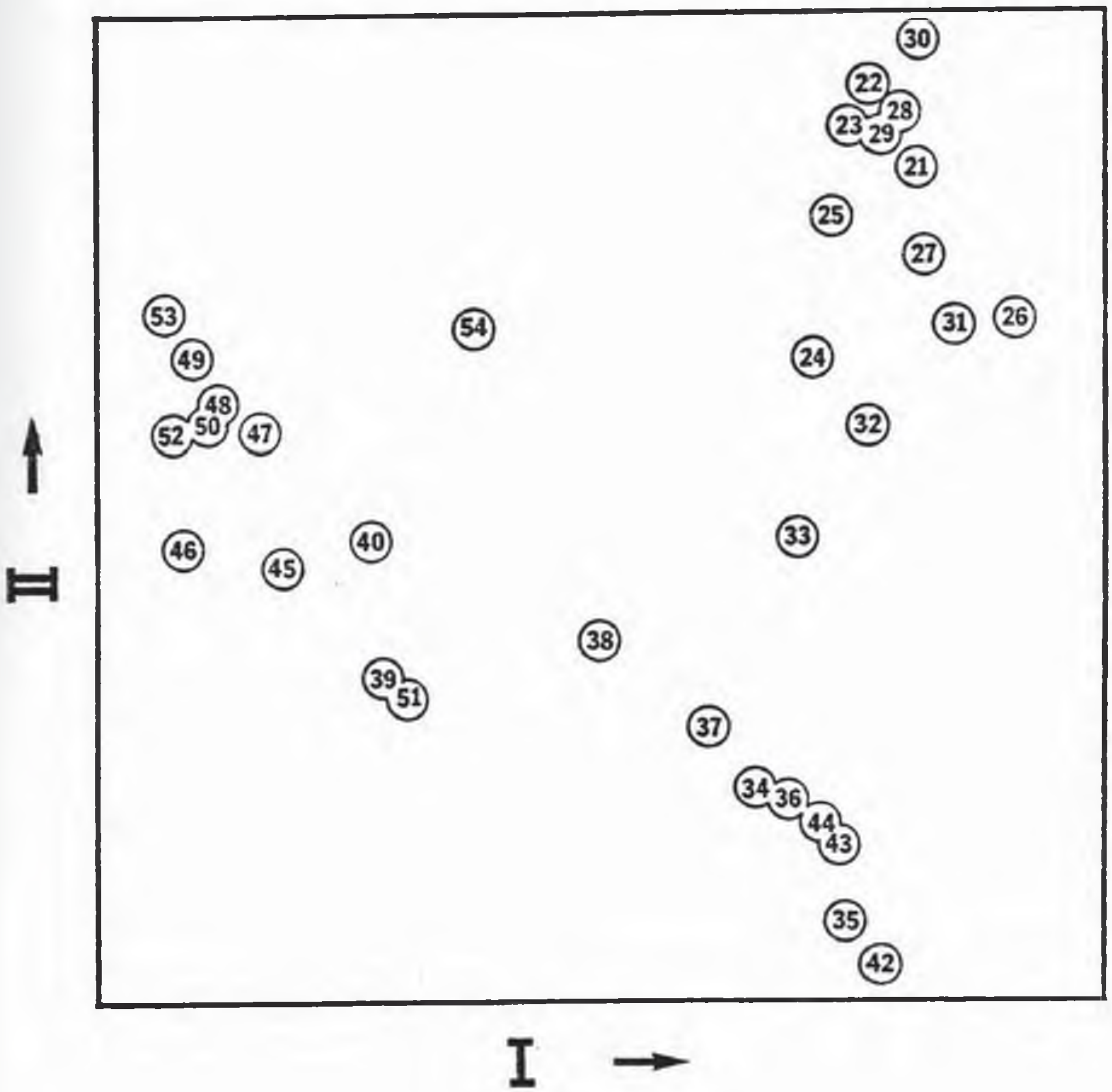
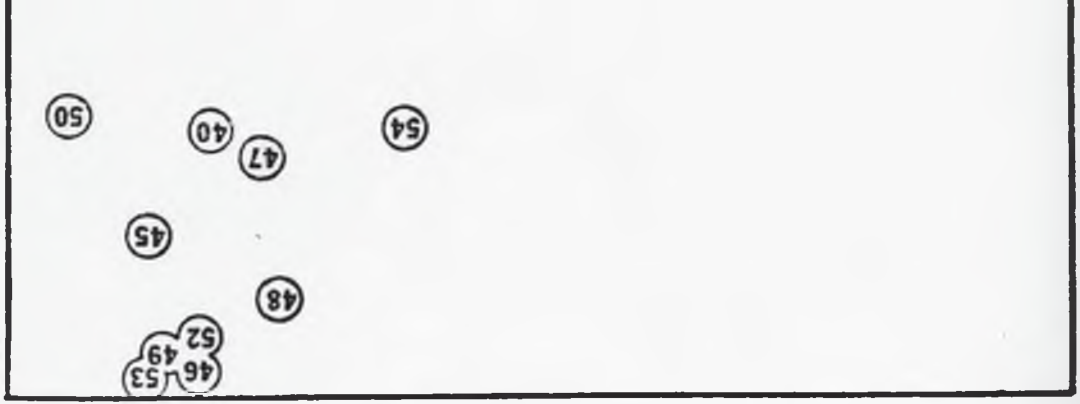

30
22
28
23
29
21
25
27
53
54
31
26
49
24
48
52
50
47
32
II
46
45
40
33
38
39
51
37
34
36
44
43
35
42
I

Figure 22. Kinosternon scorpioides females, plots of population means on first (I) vs. second (II) canonical variates.


50
40
47
54
45
48
52
49
46
53

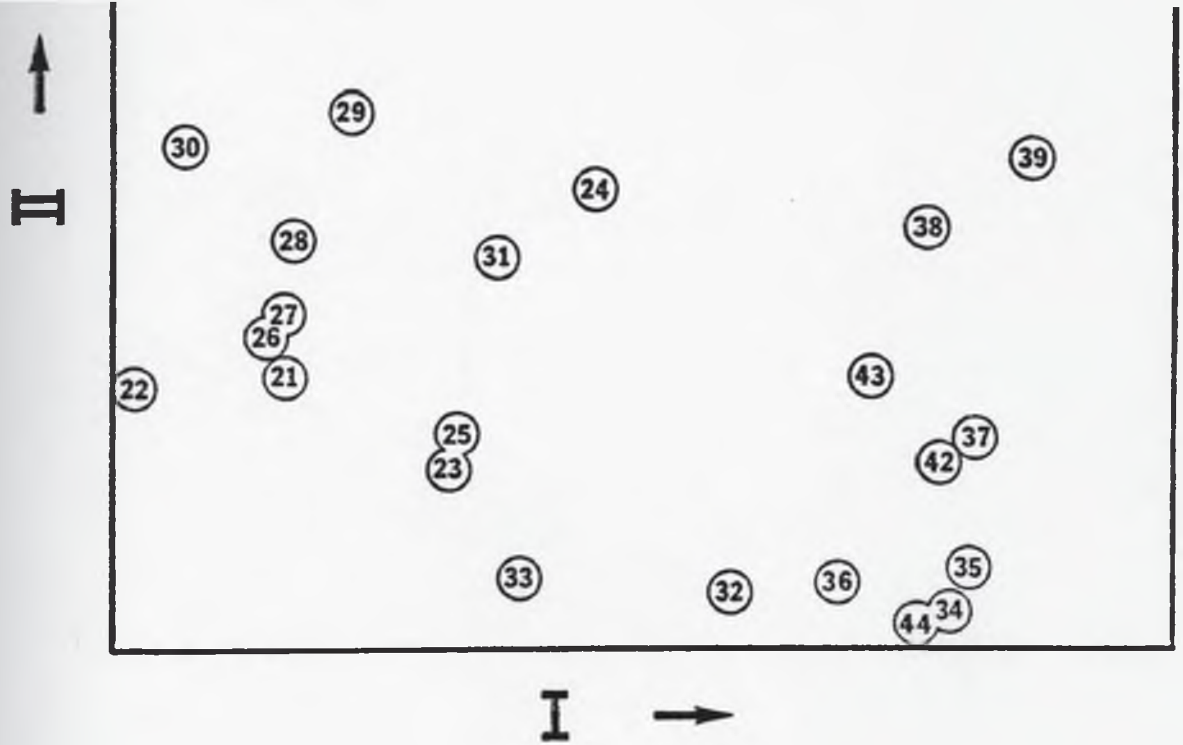

II
30
29
24
39
28
31
38
27
26
21
22
43
25
23
37
42
33
32
36
35
34
44
I

Figure 23. Kinosternon scorpioides males, dendrograph of D^2 values.

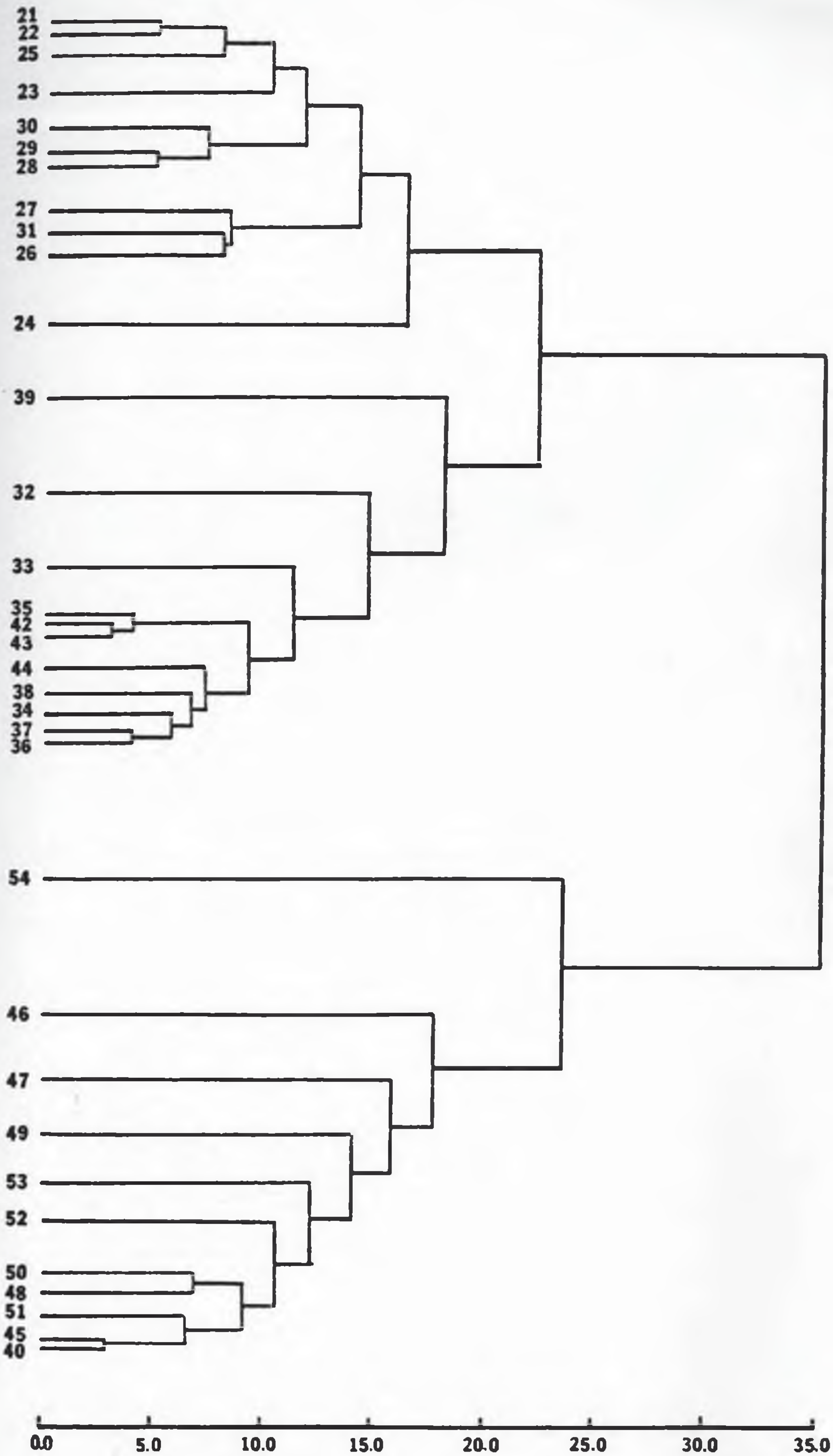
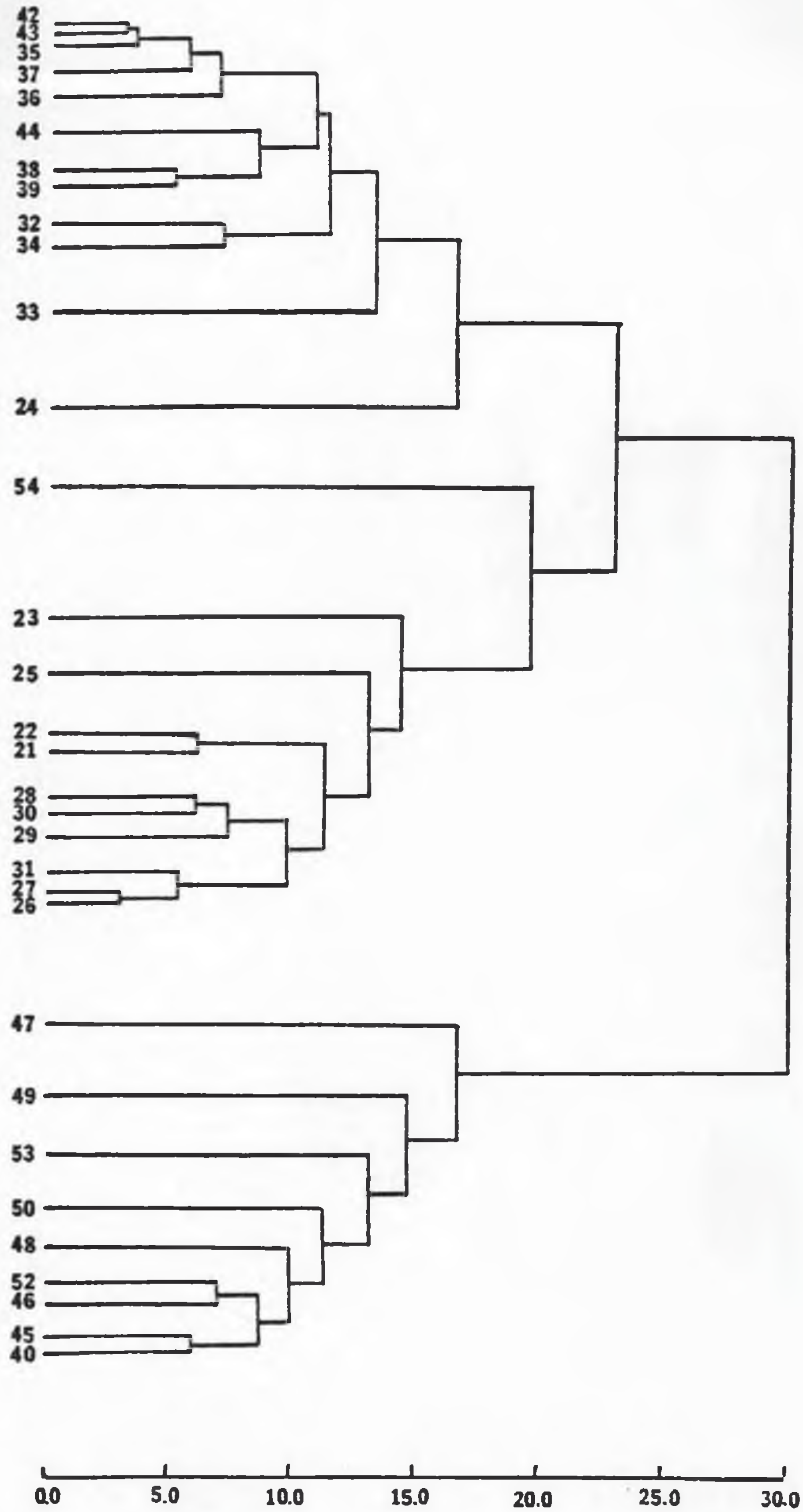

21
22
25
23
30
29
28
27
31
26
24
39
32
33
35
42
43
44
38
34
37
36
54
46
47
49
53
52
50
48
51
45
40
0.0
5.0
10.0
15.0
20.0
25.0
30.0
35.0

Figure 24. Kinosternon scorpioides females, dendrograph of D^2 values.


42
43
35
37
36
44
38
39
32
34
33
24
54
23
25
22
21
28
30
29
31
27
26
47
49
53
50
48
52
46
45
40
0.0
5.0
10.0
15.0
20.0
25.0
30.0

Population R (Río Chucanaque) is intermediate phenetically and geographically between the first mentioned group and South American populations. Population H (Corn Island) is widely separated from Mexican and Central American groups. Population I (southern Mosquito Coast) appears to be phenetically intermediate. Along the second axis, Mexican and northern Central American populations (A-G) are distinctly separate from a mid-Central American and South American group (J-U), and population I is phenetically and geographically intermediate.

Examination of the dendrograph in Fig. 15 suggests there are two major phenetically distinct groups present. The first includes populations A-G and I (Gulf of Mexico populations, and Caribbean populations southward to the southern Nicraguan Mosquito Lowlands). The second group contains two rather distinct subgroups; a group containing populations J-K and N (Nicaraguan Depression, both Caribbean and Pacific, and the Caribbean Coast of Costa Rica) and S-U (South America); and a group with populations H, L1, L2, M, R, O, and Q (Corn Island, Pacific Central America from the Osa Peninsula southward, and Caribbean drainages of northern Panamá).

Females

Along the first axis in Fig. 12 a loosely associated group is separated from group I-U (I is somewhat intermediate). Along the second axis, population H (Corn Island) is widely dispersed, while I is intermediate. Populations A and B (Ríos Mescalapa and Grijalva, northward) are separated from each other and from the other groups.

The dendrograph in Fig. 16 suggests that population B is phenetically different from the other populations. The remaining populations fall rather clearly into two discrete groups. The first is a discrete group which includes populations A (Ríos Actopán and Coatzacoalcos) and C-I (southern Gulf of Mexico drainages, and Caribbean drainages south to the southern Nicaraguan Mosquito Lowlands). Group H (Corn Island) now clusters with this northern group rather than the southern group as above. Population A is relatively discrete from the rest of this group at a level of 18.1. The second group includes populations O-U, or all populations from the Nicaraguan Depression southward to South America. In the second group, population O (Golfo de Nicoya) differs at 17.2, but otherwise there are two distinct groups of populations which differ at 15.5; a group containing populations J, K, N, U, S, T (Nicaraguan Lowlands on both Pacific and Caribbean, and South America), and a second group containing L1, L2, M, R, and Q (southern Central America).

In summary, it is evident that Kinosternon leucostomum populations fall into two phenetically distinct groups. The first of these includes populations A through G; i.e., those populations occupying the Atlantic versant of southern México and Central America from the northern limit of the species' range in the Río Actopán basin in Veracruz, Mexico, south to the Río Cuculaya basin in the Nicaraguan Mosquito Lowlands. Population I (Mosquito Lowlands) is phenetically intermediate between these and the K. leucostomum populations to the south. The population inhabiting Corn Island, Nicaragua, is phenetically distinctive, but appears to have its greatest affinities with population I on the mainland to which it is geographically closest.

The second major group of K. leucostomum includes all remaining populations in mid and southern Central America, and northwestern South America. Two distinctive "subgroups" exist within this group; the first of these includes populations L1, L2, M, O, Q, and R (vicinity of the Panama Canal, eastward throughout the Isthmus of Panamá). The second "subgroup" includes populations J, K, and N to the immediate north (Caribbean and Pacific) of the first and S, T, and U to the immediate southeast (South America), such that the first "subgroup" is geographically enclosed by the second. There is some evidence that populations O and Q-R are intermediate between the first and second "subgroups" to the north and south respectively. Population L2 (Río Chagres) shows close affinities to the Panama Canal population (L1). The population in Goofy Lake (Q) also has strongest affinities to those in the Panama Canal.

Sexual Dimorphism

The use of characters involving tail morphology has been avoided in this study, but the tail in all Kinosternon is strongly sexually dimorphic. The tail in males is long (from base to tip > 1/2 the length of the posterior plastral lobe) and prehensile, as an adaptation to assure intromission during coitus (Mahmoud, 1967; Lardie, 1977). The tail of females is short and stubby (< 1/2 maximum plastral lobe length.

Comparisons of the mean values for each character allows a determination of the relative degree of sexual dimorphism in each character (a difference in means of 0.3 or more was arbitrarily chosen as strong sexual dimorphism; a difference of 0.2-0.3 was considered weaker sexual dimorphism; for qualitative characters the difference was divided by the maximum possible value and the above criteria used to determine degree of dimorphism).

The most sexually dimorphic characters in Kinosternon integrum are as follows: CWN (males > females) suggesting females are on average widest near the middle, males slightly posterior; PHW (females > males), the plastron of males is narrower at the posterior hinge; ANL (females > males), males have shorter anul scutes on average which results from an overall shorter posterior lobe and more emarginate anal notch which presumably allows greater mobility of the tail during mating; SHT (females > males), the shell of females is relatively higher than that in males which (combined with the greater width nearer the middle of the shell) reflects the generally more circular cross section of the shell of females, and the tendency for the plastron in males to be flat or concave; AIC (females > males), females have more frequent contact between the axillary and inguinal scutes due mainly to a larger inguinal scute, which may be involved in strengthening a potential structural weak spot in the bony shell which the inguinal crosses, namely the sutures between the hyoplastron and hypoplastron, and the peripheral bones 5-7; and M11 (males > females), the significance of which is difficult to interpret, but may be the result of an ontogenetic pattern (M10 and M11 are the same height, or M11 is slightly higher in small individuals) in that females are on average smaller than males, or conceivably from a greater demand for structural support posteriorly in females.

Less dimorphic characters (differences of 0.2-0.3) are CWA and

CWP (females > males) which suggests the relatively greater width of females at M5 and M8; and AHW, TFW, BRL, and INL (females > males in all) which demonstrates the overall proportionately more extensive plastron of females.

The pattern of sexual dimorphism in Kinosternon scorpioides is similar to that for K. integrum, although fewer characters show significant dimorphism. As in integrum, SHT, AIC and M11 show strong dimorphism (> 0.3). Unlike integrum, there is also strong dimorphism in SIM (females > males), which is also difficult to assess although it is conceivable that supernumerary inframarginal scales in females could help give structural support at the suture between the hyoplastron, hypoplastron, and peripheral bones. Characters in K. scorpioides which show less strong sexual dimorphism (difference of 0.2-0.3) include C5L (females > males), suggesting females have a longer fifth central scute than males (also reflected in smaller M11 in females as discussed above); and CWA, ABL, PHW, TFW, ANL, and BRL (females > males in all) which demonstrates the same pattern seen in integrum; that is, the carapace of males is proportionately narrower, the bridge shorter, and the plastron generally smaller than in females.

The patterns of sexual dimorphism in Kinosternon leucostomum are generally similar to the above, but even fewer characters show significant dimorphism. The only strongly dimorphic character is M11 (females > males). Less dimorphic characters (difference 0.2-0.3) are PHW, TFW, ANL, and SHT (females > males in all), and C5L (males > females), the significance of all were discussed above.

The relatively globular shell of females in all taxa under consideration, as evidenced by greater CWA, CWP, and SHT, is a shape which would increase internal volume presumably for eggs and follicle storage. The relatively smaller plastron of males probably allows greater mobility of the limbs and tail during mating, while the relatively more extensive plastron of females may (1) provide protection during nesting from small predators (e.g., Shealey, 1976 discussed small animal predation on nesting Graptemys), and/or desiccation (kinosternids were found to be less resistant to desiccation than other turtles by Bogert and Cowles, 1947, and Ernst, 1968); or (2) help protect females from injury inflicted by males during vigorous mating attempts (males bite and claw females, sometimes savagely, during mating cf. Sexton, 1960; Mahmoud, 1967 and Lardie, 1977). Consistent with these explanations are the facts that in those populations in which the male plastron is smallest (populations 8B, 10, 13, 15-17, 20B, and 39-53), the dimorphism is greatest; that is, females still maintain relatively large plastrons. In populations in which males have extensive plastrons, there is often very little dimorphism in plastron size suggesting similar selection pressures on both sexes (i.e., males are subject to the same terrestrial selective pressures as females).

EVOLUTION OF PLASTRON SIZE

The discriminant analyses used in this study have demonstrated the importance of a series of intercorrelated characters which show that in some populations of *K. integrum*, *K. scorpioides*, and *K. leucostomum* (or in females *vs*. males in most populations), a high, wide carapace is associated with an extensive plastron. Conversely, some populations have relatively low, narrow carapaces and small plastrons.

It has been suggested (Berry, 1977; D. M. Bramble, pers. comm.) that the high, wide shell and extensive plastron in *Kinosternon* constitutes a "box turtle syndrome"; i.e., natural selection favors a box turtle morphology in individuals which leave the water periodically by providing protection from small predators or desiccation or both during periods of terrestriality. In permanent-water situations, natural selection should favor reduced plastrons to increase motility of the limbs (kinosternids are "bottom walkers", Zug, 1971). Legler (1960), Shah (1960), Richmond (1964), and Bramble (1974) have discussed the morphological adaptations associated with plastral kinesis and the "box turtle syndrome."

The following test of the above hypothesis was designed. Specimens of *Kinosternon scorpioides* and *K. leucostomum* complex members which had been prepared as dry shells were accumulated. The ventral surfaces of these specimens were then photocopied using a Xerox model

3100LDC photocopier with a flat glass plate. Each shell was photocopied twice; once each with the portion of the shell anterior to the anterior hinge, and again with the portion posterior to the anterior hinge, pressed flat against the glass. This helped to minimize distortion otherwise present due to the difference in planes of the two portions of the shell. These two photocopies were then attached at the anterior hinge region providing a two dimenstional representation of both the ventral carapace and plastron.

The total area occupied by the outline of the ventral carapace and by the plastron were then calculated using a standard polar planimeter. A ratio was calculated by dividing the former value into the latter, which provided a number which is the proportion of the ventral carapacal outline occupied by the plastron. In other words, this technique provides an accurate measure of the size of the plastron relative to the carapace.

The range of values of relative plastron size and means for both sexes in each population sampled is shown for *K. scorpioides* and *K. leucostomum* complex members (both sexes) in Fig. 25. It is clear that specimens from some populations (e.g., Canal Zone *vs*. Lake Nicaragua *scorpioides*) have proportionately smaller plastrons than others. In general, females have larger, less geographically variable plastrons than males.

In order to determine the relative importance of various environmental variables in predicting the relative size of the plastron, relative plastron size values were used in multiple regression analyses as the independent variable (computer program BMD02R, Dixon, 1973, was used). Independent variables in these analyses were determined (as closely as possible) for each locality from which specimens were collected. They include latitude (to the nearest degree) and elevation (to the nearest 100 m) gathered from American Geographic Society topographic maps (1:1,000,000); mean annual rainfall, yearly rainfall variability, mean precipitation for March, mean precipitation for September, mean humidity for March, mean humidity for September, and mean annual temperature, all extrapolated from maps and isoclines in Vivó Escoto (1964); number of sympatric turtle species (from a variety of sources); and a relative "permanence index" for the aquatic habitat from which the turtles were collected, which ranged from "1" if the turtles were collected in a permanent aquatic habitat, to "5" if they were collected on dry land over 100 m from water (these subjective values were determined from the unpublished field notes of J. M. Legler, E. O. Moll, F. V. Nabrotsky, and J. L. Christiansen).

The results of the multiple regression analyses, run independently for males and females, are shown for _K. scorpioides_ in Table 39, and for _K. leucostomum_ in Table 40. In males of both species, "permanence index" was the character selected first, and with the highest r^2 value (roughly equivalent to the proportion of the variance explained by that character). In females of _K. scorpioides_ the permanence index was selected first, but its r^2 value is much lower than in the analyses of males (0.65 as opposed to 0.94 and 0.91). The permanence index was selected second in the analysis of female _leucostomum_, but the character selected first was mean precipitation for March (at mid-dry season) and is probably a component of the permanence index.

The results of the analyses are consistent with the hypothesis proposed. It is likely that a "box turtle"-like shell with a large plastron is an adaptation to seasonal aquatic situations. The correlation is less clear in females than in males, probably because females of even the most aquatic populations must occasionally leave the water to nest, and natural selection would favor a more extensive plastron during these brief terrestrial periods.

Figure 25. Range (horizontal line) and mean (vertical line) for relative plastron sizes (plastron area/carapace area) for *Kinosternon scorpioides* and *K. leucostomum* complexes.

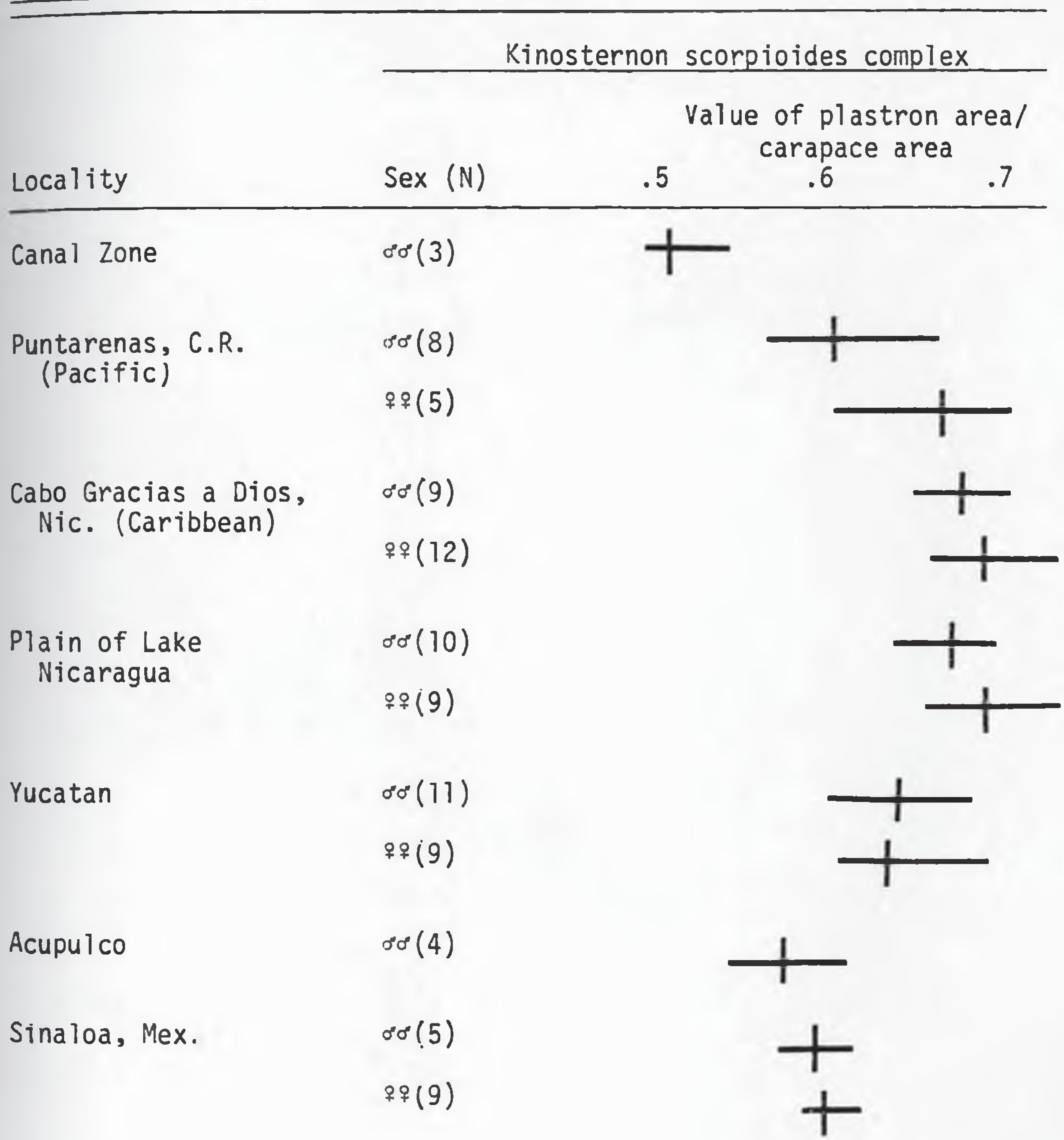


Figure 25 (continued)

Locality	Sex (N)	Kinosternon leucostomum complex: Value of plastron area/ carapace area (.5 – .6)
Ailigandi, San Blas, Panama	♂♂(6)	
	♀♀(3)	
Canal Zone	♂♂(12)	
	♀♀(4)	
Almirante, Bocas del Toro, Panama	♂♂(10)	
	♀♀(9)	
Cabo Gracias a Dios, Nicaragua	♂♂(6)	
	♀♀(4)	
Alvarado, Veracruz, Mexico	♂♂(5)	
	♀♀(9)	

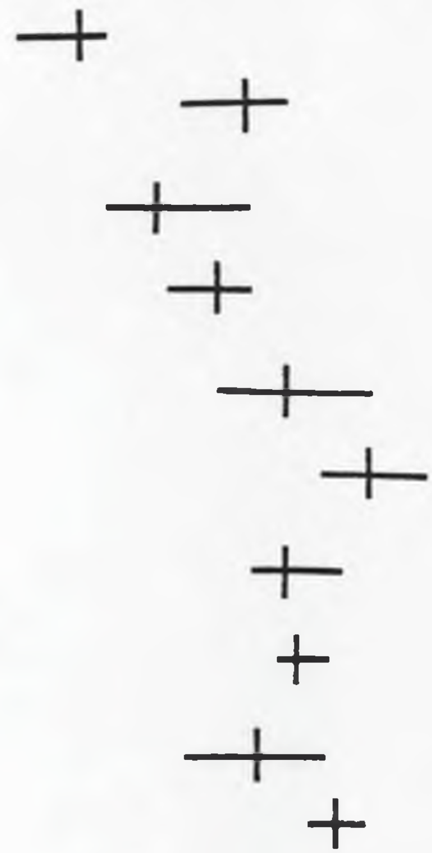


Table 39. Environmental variables added to multiple regression on relative plastron area for Central American *Kinosternon scorpioides* and *K. integrum*.

	r^2	Increase in r^2
Males		
1. Permanence index	.9373	.9373
2. $\bar{X}$ precipitation for September	.9515	.0142
3. Elevation	.9567	.0051
4. $\bar{X}$ precipitation for March	.9592	.0025
5. $\bar{X}$ annual temperature	.9603	.0011
6. $\bar{X}$ humidity for March	.9611	.0008
Females		
1. Permanence index	.6462	.6462
2. Latitude	.7956	.1495
3. $\bar{X}$ annual rainfall	.8364	.0407
4. Elevation	.8745	.0381
5. $\bar{X}$ precipitation for September	.9035	.0290
6. $\bar{X}$ variability in rainfall	.9059	.0024

Table 40. Environmental variables added to multiple regression on relative plastron area for Central American *Kinosternon leucostomum*.

	r^2	Increase in r^2
Males		
1. Permanence index	.9069	.9069
2. Elevation	.9817	.0748
3. Number of sympatric species	.9900	.0083
4. $\bar{X}$ annual rainfall	.9998	.0098
5. Latitude	.9999	.0001
6. $\bar{X}$ annual temperature	.9999	.0000
Females		
1. $\bar{X}$ precipitation for March	.8336	.8336
2. Permanence index	.9678	.1342
3. $\bar{X}$ precipitation for September	.9960	.0282
4. Elevation	.9998	.0038
5. Latitude	.9999	.0001
6. $\bar{X}$ annual rainfall	1.0000	.0001

SYSTEMATIC ACCOUNTS

The following systematic arrangement of the turtles of the *Kinosternon scorpioides* and *K. leucostomum* complexes is based on relationships among populations as determined by the phenetic analyses presented above. Populations or groups of populations which were shown to be significantly and consistently discrete are generally recognized as distinct taxa. Comments on new or unique taxonomic arrangements follow each account.

The *Kinosternon scorpioides* complex is considered to consist of four closely related species in México and Central America; *K. integrum*, *K. alamosae*, *K. oaxacae*, and *K. scorpioides* (the last mentioned with four subspecies north of continental South America, *K. s. cruentatum*, *K. s. abaxillare*, *K. s. albogulare*, and *K. s. scorpioides*). The *K. leucostomum* complex consists of but a single species with two subspecies; *K. l. leucostomum* and *K. l. postinguinale*.

For each taxon a complete, chronological list of synonyms is given. Each list includes all names which are considered to be junior synonyms for the taxon, with references to the original user of the name and subsequent users whose work is of taxonomic importance. References with the synonyms are given as author, date, and page number; complete references are given in the literature cited section.

The diagnoses and descriptions of the various taxa are based on characters shown by the multiple discriminant analyses to be most important in accounting for patterns of geographic variation observed.

Unless otherwise indicated, values for each character in the diagnoses and descriptions are given as a proportion of CL. Relative plastral extent is expressed as "plastral index" (devised by J. M. Legler, unpublished), which consists of mean values of AHW as a proportion of CWA, and mean TFW as a proportion of CWP separated by a slash (e.g. the plastral index for K. integrum males is .77/.68, or plastral width at the anterior hinge and mid-femoral scute averages 77% and 68% of the widths of the carapace at the same respective levels). Average lengths of plastral scutes at the midline, expressed as a proportion of CL, are given in order from anterior to posterior (i.e. gular-humeral-pectoral-abdominal-femoral-anal). Character values (mean and range) useful in distinguishing the taxa are given in Tables 41-43.

Diagnoses of the family Kinosternidae and genus Kinosternon precede the specific and subspecific accounts. Characters considered diagnostic at the familial or generic levels are not mentioned in the diagnoses or descriptions of species and subspecies.

Family Kinosternidae: Diagnosis

Members of the family Kinosternidae can be distinguished from members of other families of the chelonian suborder Cryptodira by the following combination of characters: (1) eleven marginal scutes on each side (excluding precentral); (2) tenth marginal scutes (M10) distinctly higher than M7-M9 (except Kinosternon flavescens with M9 and M10 distinctly higher than M7-M8); (3) carapacal scutes imbricate; (4) two pairs of musk glands present, with ducts opening into axillary (M1-M3) and inguinal (M7-M8) regions; (5) one to six pairs of gular barbels; (6) four to sixpairs of papillae on neck and tail; (7) hands and feet fully webbed; (8) digits 1-5 of hands and 1-4 of feet bearing claws; (9) tails of males elongate, prehensile, not as long as the posterior plastral lobe, but greater than 1/2 the length of the lobe; tails of females less than 1/2 the length of the posterior plastral lobe; (10) ten peripheral bones on each side (excluding nuchal); (11) nuchal bone with well-developed costiform processes; (12) five to seven neural bones present; (13) second cervical vertebra opisthocoelous, third biconvex, eighth concave in front; (14) frontal bones not entering rim of orbit; (15) maxilla contacting quadratojugal; and (16) stapedio-temporal foramen reduced or absent.

Genus Kinosternon: Diagnosis

Members of the genus *Kinosternon* can be distinguished from other kinosternid genera (*Sternotherus*, *Staurotypus*, *Claudius*) by the following combination of characters: (1) plastron with two transverse, freely kinetic hinges bordering anterior and posterior margins of the abdominal scutes (anterior edge of hyoplastral bone, and posterior edge of hypoplastral bone); (2) gular scute well developed, never shortest plastral scute at midline; (3) tails of males and females with terminal horny spines, larger in males than in females (except in *K. angustipons* in which tails in both sexes lack spines); (4) entoplastral bone absent; and (5) five to six neural bones present.

Kinosternon integrum Le Conte (Fig. 26)

Kinosternum integrum Le Conte, 1854:183. Type locality: "Mexico". (Restricted by Smith and Taylor, 1950b to Acapulco, Guerrero, México.)

Thyrosternum integrum Agassiz, 1857:429.

Cinosternon integrum Strauch, 1862:1; Bocourt, 1876:393.

Swanka integra Gray, 1870:69.

Cinosternon rostellum Bocourt, 1876:391. Type locality: Guanajuato, Mexico.

Cinosternon guanajuatense (nomen nudum) Duges, 1888:107; Smith, 1969: 110.

Cinosternum integrum Cope, 1887:23; Boulenger, 1889:42.

Kinosternon integrum Stejneger, 1899:64; Smith and Taylor, 1950a:331; 1950b:25; Mertens and Wermuth, 1955:337; Casas Andreu, 1965:386; Duellman, 1961:58; Hardy and McDiarmid, 1969:104.

Cinosternum scorpioides integrum Siebenrock, 1906:96; 1909, 445.

Cinosternum scorpioides integrum forma *mexicana* (nomen illegitimum) Siebenrock, 1907:576.

Kinosternon scorpioides integrum Ahl, 1934:184; Wermuth and Mertens, 1961:25; Casas Andreu, 1967:47; Pritchard, 1967:40; Morafka, 1977:70.

Diagnosis

Kinosternon integrum attains large adult size (males to 202 mm CL, females to 188 mm CL), and can be distinguished from all other Mexican and Central American *Kinosternon* by the following combination of characters in adults: (1) clasping organs (Legler, 1965) lacking; (2) carapace intermediately or weakly tricarinate, keels frequently lost in oldest, largest individuals; (3) plastron intermediate to extensive, may or may not completely close ventral opening of shell (plastral index: ♂♂ =.77/.68, ♀♀ = .78/.70); (4) interanal seam length greater than 2/3 posterior plastral lobe length; (5) posterior plastral lobe with variously emarginate anal notch, somewhat more emarginate in males than females but rarely lacking; and (6) M11 flared outward (*i.e.* posteriorly) in profile; not vertical.

Description

Carapace of intermediate width (CWA = ♂♂ .61, ♀♀ .63; CWP = ♂♂ .63, ♀♀ .66), and intermediate height (SHT = ♂♂ .36, ♀♀ .39). Widest point on carapace at mid-M7 in males, and posterior M6 in females (CWN = ♂♂ 7.09, ♀♀ 6.75). Carapace with weak to intermediate keels (DKL = 0.90, DKC = 1.19), frequently lost in oldest and largest individuals. C1 usually (89% of males, 92% of females) contacts M2. Central scutes variable in size. Precentral scute small, longer than wide dorsally and ventrally in 98% of individuals examined. M10 usually higher than M11. Margin of carapace flared from M8 to M11.

Plastron intermediate to extensive (AHW = ♂♂ .46, ♀♀ .49; TFW = ♂♂ .43, ♀♀ .46), may or may not completely close ventral openings. Anal notch variable but almost always emarginate, more emarginate in males than in females. Posterior hinge curved posteriorly (Fig. 26). Bridge intermediate in length (BRL = .25), lacking longitudinal grooves. Interlaminal seams of plastron at midline: ♂♂ = .16-.12-.05-.26-.08-.22, ♀♀ = .16-.12-.05-.28-.08-.25.

Dorsal head shield V-shaped, bell shaped, or triangular (apex anterior). Maxillary sheath variably hooked, hook better developed in males than in females or immature specimens. Three to five pairs of gular barbels present, anteriormost pair (nearest mandibular symphysis) largest, posterior pairs smaller but of subequal length. Clasping organs lacking from hind leg and thigh.

Color and pattern

Color and pattern of carapace and plastron extremely variable. Carapacal ground color variably straw, yellow, olive, brown or black, or mottled combinations of these. In pale specimens, interlaminal seams usually darker. Larger specimens frequently with dark brown or black flecks 10-50 per scute, often arranged in short dorsolateral stripes. Plastral pattern pale yellow, cream or yellow; interlaminal seams darker.

Dorsal and lateral head pattern variable. Northern Pacific Coast populations (1B-5) with series of pale cream to yellow, and brown to black postorbital blotches, often coalescing to form vague postorbital stripes. Southern Pacific Coast populations with head pattern consisting of variously mottled or reticulated brown to black and cream to yellow, often with a faint postorbital stripe following angle of upper jaw. Río Lerma populations (9A-11A) with head pattern consisting of faint postorbital stripe only, or only vague reticulate pattern.

Ventral surface of head and neck cream to yellow or brown, with pale gray or brown spots or immaculate. Jaws of males vertically streaked with brown or black, those of females faintly streaked or immaculate. Other soft parts (limbs, neck, and tail) dark gray or brown above, pale gray, cream, or yellow beneath.

Geographic range

The geographic range of Kinosternon integrum is shown in Fig. 4. Along the Pacific Coast of México, the distribution is continuous from the Río Yaqui in the north to the Río Verde in the south. The northern limit of the range corresponds to the limit of the range of the Tropical Thorn Scrub vegetational community, which is the northern limit of the geographic ranges of a number of predominantly tropical vertebrates (Stuart, 1964). This northern limitation results from the interruption of the coastal plain at a point where a small line of hills (Cerro de Guaymas) extends from the Sierra Madre Occidental to the Gulf of California. Specimens referred to K. integrum from localities north of the Cerro de Guaymas at about 29° N latitude (see Morafka, 1977 map 27) are referrable to other species of Kinosternon.

The northernmost point at which the range of K. integrum breeches the Sierra Madre Occidental is the Río Mezquital (San Pedro), from which the range extends northward and eastward from western Nayarit into Durango. The next major drainage southward to breech the Sierra Madre is the Río Grande de Santiago through which populations on the northern Pacific Coast and those on the Mexican Plateau are in communication. K. integrum occurs throughout the Río Lerma-Santiago system, which includes most of the external drainages of the southwestern Mexican Plateau.

The bulk of the eastern Mexican Plateau is drained by the Río Pánuco-Tamesí system which is inhabited by integrum only at elevations above 800 m. Even though the Sierra Madre Oriental is breeched in several places by the Ríos Pánuco and Tamesí and their tributaries (and the eastern Plateau and Gulf Coast thus brought into contact), it appears that K. integrum is completely replaced by K. scorpioides at elevations below 500 m (Iverson and Berry, MS). Martin (1955) discussed specimens of integrum from the upper Río Tamesí, but specimens now available from the Río Chihue (see Iverson and Berry, MS) establish the northern tributaries of the Río Tamesí as the northern limit of the range on the eastern Plateau. Elsewhere, K. integrum is known from Gulf of Mexico drainages only in the upper portions of the Río Papaloapan above 1000 m elevation, below which it is ultimately replaced by K. scorpioides.

The southernmost limit of the range of K. integrum appears to be the Río Verde system in Oaxaca, México. To the east, it is replaced by K. oaxacae in the Ríos Colotepec and Tonameca, and by K. scorpioides in the Río Tehuantepec eastward. K. integrum inhabits most of the Pacific drainages along the narrow southern Pacific Coast. Southern and northern Pacific Coast populations are discretely separated by the Sierra Volcánica Transversal in Coastal Jalisco. K. integrum occurs throughout the Río Armería, Coahuayana, and Balsas systems which drain most of the southern portion of the Mexican Plateau.

Specific localities for Kinosternon integrum are listed by Anderson and Lidicker (1963), Berry and Iverson (MS), Berry and Legler (MS), Bogert and Oliver(1945), Casas Andreu (1967), Conant (1969), Davis and Dixon (1961), Davis and Smith (1953), Dixon, Ketchersid, and Lieb (1972), Duellman (1954, 1961, 1965), Grant and Smith (1959), Greene (1972), Hardy and McDiarmid (1964), Heringhi (1969), Iverson and Berry (MS), Martin (1955), Martin del Campo (1942), McDiarmid (1963), Morafka (1977), Oliver (1937), Peters (1954), Slevin (1926), Smith and Van Gelden (1955), Snyder (1972), Stejneger (1899), Taylor (1952), Van Denburgh and Slevin (1914), Webb and Hensley (1959), Zweifel (1960), and Zweifel and Norris (1955).

Specimens of Kinosternon integrum reported from South America

(Siebenrock, 1907; Ruthven, 1922) are referrable to _Kinosternon_ _s_. _scorpioides_.

Natural history

Kinosternon _integrum_ has been collected in virtually every type of slow moving aquatic freshwater habitat throughout its range. Duellman (1961) found it in "all permanent and temporary ponds, lakes, and streams below 2200 meters" except Lago de Patzcuaro in Michoacán, México. Hardy and McDiarmid (1969) found it to be the commonest turtle in Sinaloa, México, occurring in "ponds, ditches, and on the road at night" in all river drainages in the state. These general observations have been confirmed by field observations in the Mexican states of Sonora, Sinaloa, Nayarit, Jalisco, Michoacán, and Guerrero (unpublished field notes of J. F. Berry, J. L. Christiansen, J. M. Legler, E. O. Moll, and F. V. Nabrotsky).

J. M. Legler (pers. comm.) collected 80 _K_. _integrum_ representing 40-50% of those present from a 10 x 10 m impoundment near Alamos, Sonora on 19-26 May 1978 during an extremely dry period. I found _K_. _integrum_ to be abundant in arroyos and ditches adjacent to Lago de Chapala in Jalisco, México at the beginning of the rainy season (24-27 June 1975), but absent from the lake itself.

_K_. _integrum_ has been collected in association with all vegetational communities except the most xeric or montane in Jalisco (Hardy and McDiarmid, 1969), Michoacán (Duellman, 1965), Colima (Duellman, 1958), Guerrero (Davis and Dixon, 1961), and Sonora (Heringhi, 1969). Webb and Hensley (1959) reported a collection of _integrum_ from a mountainous area of pine, oak, madraño, and manzanita at 8350 ft

(2545 m) in intermittent pools near the headwaters of the Río Grande de Santiago in Durango, México.

Remarks

Aside from populations 1A (K. alamosae) and 20B (K. oaxacae), which are considered in this report to be distinct species and will be discussed below under their own systematic accounts, population 8B (Río Purificación, Jalisco) is the most phenetically distinct population of K. integrum analyzed. Adult individuals from population 8B differ from those of other K. integrum populations in several characters which are summarized in Table 41 below.

Table 41. Comparison of population 8B to other populations of Kinosternon integrum.

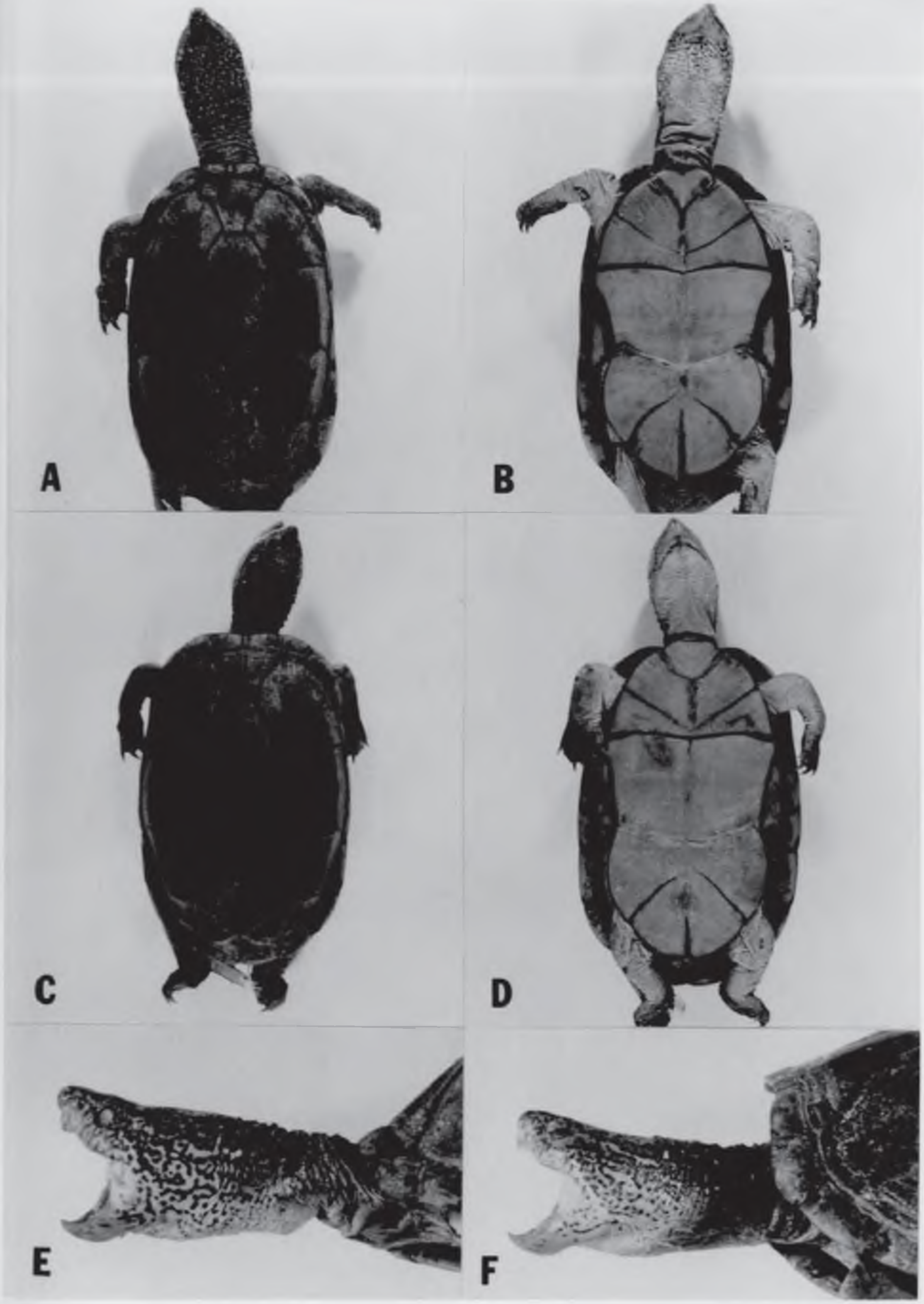
Population 8B	K. integrum
Ci narrow (C1A/C1L = 0.84).	C1 wide (C1A/C1L = 1.05).
Carapace faintly keeled.	Carapace strongly to weakly keeled.
Plastron small (plastral index = ♂♂ .66/.65, ♀♀ .70/.59).	Plastron generally extensive (plastral index = ♂♂ .77/.64, ♀♀ .77/.66).
Axillary and inguinal scutes in broad contact.	Axillary and inguinal scutes in narrow contact, or contact lacking.
Adult size small (♂♂ to 106 mm CL, ♀♀ to 103 mm CL).	Adult size large (♂♂ to 202 mm CL, ♀♀ to 188 mm CL).
Interfemoral seam long (FEL > 0.1 of CL).	Interfemoral seam variable (FEL usually < 0.1 of CL).

It appears likely that population 8B has been isolated in coastal Jalisco by the Sierra Madre Occidental, where lack of gene flow with outside populations has permitted differentiation. The precise relationships between population 8B and other K. integrum populations must, however, await the collection of larger comparative series of specimens (8B is represented by only 5 specimens in this study).

Other K. integrum populations are more similar phenetically to each other than any is to population 8B. Nevertheless, those populations in the southern Pacific Coast of México (populations 10, 14-16, and 20A) are phenetically distinct from those from the northern Pacific Coast of México and the Mexican Plateau. As noted in the discriminant analyses, populations from the southern Pacific Coast have flatter, narrower shells (small SHT, CWA and CWP), smaller C1L, C1A, C3L, smaller plastrons (GUL, AHW, PHW, TFW, ABL, BRL, INL, FAW, and HPW), and more prominent keels (larger DKL and DKC). AXL is largest in southern populations. Those populations from the upper Río Balsas (18) are most similar to Mexican Plateau populations, while those from the mid-Balsas (17) are intermediate.

Siebenrock (1907) considered integrum to be a subspecies of K. scorpioides, although he felt the name "integrum" also applied to populations in northern South America. Several recent authors have also considered integrum a subspecies of scorpioides (Wermuth and Mertens, 1961; Casas Andreu, 1967, Pritchard, 1967; Morafka, 1977). Two forms of evidence argue against this arrangement: (1) K. integrum and K. scorpioides both occur in the Río Pánuco and Río Papaloapan basins in eastern México, although they are not known to occur at the same locality (they occur within 40-50 km, and are separated by

Figure 26. Dorsal, ventral, and head views of Kinosternon integrum male (A-B, E: UU 7778, CL = 176 mm), and female (C-D, F: UU 7783, CL = 163 mm, both from Río San Lorenzo, 17 mi ENE El Dorado, Sinaloa, México). Head views X.56.


A
B
C
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F

200-300 m elevation); and (2) there is no evidence of morphological intermediacy which might imply intergradation or hybridization, or clinal variation, or any other evidence of racial variation (in fact, inspection of the appropriate table shows that Mexican scorpioides are more different from integrum than are scorpioides from anywhere alse in the range of the species). I cannot agree with Morafka's (1977) suggestion that integrum represents a "Mexican high Plateau race of scorpioides", since integrum occurs at elevations to sea level along Pacific Coastal Mexico. Kinosternon integrum is here regarded as a species closely related to but specifically distinct from K. scorpioides.

Kinosternon alamosae Berry and Legler

(Fig. 27)

Kinosternon integrum (in part) Bogert and Oliver, 1945:396; Langebartel and Smith, 1954:126; Zweifel and Norris, 1955:248.

Kinosternon alamosae Berry and Legler, MS. Type locality, Rancho Carrizal, 7 mi (11.3 km) W Alamos, Sonora, México.

Diagnosis

Kinosternon alamosae is a medium-sized Kinosternon (males to 135 mm CL, females to 126 mm CL) most similar to K. integrum, but with the following unique combination of characters in adults: (1) carapace rounded, non-carinate; (2) plastron extensive, completely closing ventral openings of the shell (plastral index: ♂♂ .79/.70, ♀♀ .79/.74); (3) anal notch small or lacking; (4) axillary and inguinal scutes widely separated, inguinal narrowly contacting M6, never contacting M5; (5) posterior carapace only slightly flared outward (i.e. posteriorly), nearly vertical in profile; (6) C1 narrow, usually not contacting M2 (in 88% of individuals); (7) clasping organs lacking; and (9) carapace without keels, or with very faint keels.

Description

Carapace relatively narrow (CWA = ♂♂ .61, ♀♀ .63; CWP = ♂♂ .63, ♀♀ .65), oval in dorsal aspect with faint keeling or unkeeled. A longitudinal depression, roughly the width of the central scutes, evident on the dorsum of females. C1 narrow, not or barely in contact with M2. Margin of carapace flared posteriorly at M8-M10, but nearly vertical in profile at M11.

Plastron extensive, completely or almost completely closing ventral openings of shell (AHW = ♂♂ .48, ♀♀ .50; TFW = ♂♂ .44, ♀♀ .48). Posterior plastral hinge curved posteriorly (Fig. 27 B, D). Plastral lobes rounded, anal notch small or absent. Plastron concave in males, convex or flat in females. Posterior plastral lobe longer in females than in males, protruding nearly to posterior edge of carapace (Fig. 27 D). Interlaminal seams of plastron at midline: ♂♂ = .16-.10-.03-.29-.08-.23, ♀♀ = .16-.10-.03-.32-.08-.26. Axillary and inguinal scutes short (AXL = .10; INL = .21). Posteriormost point of axillaries to mid-M5, anteriormost point to mid-M6. Axillary and inguinal scutes never in contact.

Dorsal head shield rhomboidal or bell-shaped; rostrum short and broad in dorsal aspect. Maxillary sheath weakly to moderately hooked. One or two pairs of short, stubby barbels present on chin, absent in some specimens. Clasping organs lacking.

Color and pattern

Ground color of carapace uniform olive to brown, sometimes partially transparent revealing bony sutures beneath. Interlaminal seams dark brown to black. Marginal scutes paler dorsally than centrals or costals.

Ground color of plastron pale to dark yellow. Interlaminal seams dark brown to black.

Skin of soft parts pale gray to brown dorsally, cream or pale gray ventrally. Skin of head with fine, dark reticulations, often coalescing into dark spots or mottling. A poorly defined postorbital stripe often present from posteroventral margin of orbit to angle of jaws. Skin of head cream or gray ventrally, bearing dark spots or immaculate. Jaw sheaths gray or brown with numerous dark streaks in males, either immaculate or with pale gray streaks in females.

Coloration in life essentially as above. Iris of live female dark orange, that of a male brown. Iris in both sexes bearing flecks of melanin forming a ruptive stellate pattern around pupil.

Geographic range

Kinosternon alamosae is known from the Pacific Coastal Lowlands in northwestern México from the vicinity of Guaymas, Sonora (Río Yaqui basin), southward at least to Guasave, Sinaloa (Río Sinaloa basin). The geographic range of *K. alamosae* is shown in Fig. 3. It is possible the range extends as far south as Culiacán, Sinaloa (Río Culiacán) based on two specimens (LACM 105396-97) bearing the tag "México: Sinaloa: Culiacán"; but these data are suspect (R. L. Bezy, pers. comm.). The geographic range of _K. alamosae_ is limited to the north by the Cerro de Guaymas which forms a barrier to dispersal between the Sierra Madre Occidental and Golfo de California. This barrier corresponds to the limit of Thorn Scrub Forest, and to the northern limit of many tropical vertebrates (Stuart, 1964). _K. integrum_ is sympatric with _K. alamosae_ in the vicinity of Alamos, Sonora (Ríos Mayo and Fuerte).

Natural history

Little is known of the natural history of _K. alamosae_. Heringhi (1969) collected specimens of _Kinosternon_ (including _alamosae_) in a drying, odorous cattle reservoir in soft mud, and in clear pools and shaded shores in leaf litter along a sandy wash, all associated with Short Tree Forest (Gentry, 1942) communities near Alamos, Sonora. Unfortunately, he did not distinguish between the habits of _integrum_ and "_hirtipes_" (_alamosae_) but stated that the two species "do not separate geographically". Wiewandt _et al_. (1972) show a photograph of a temporary pond near Alamos in which "_Kinosternon sonoriense_" (possibly _alamosae_, but almost certainly not _sonoriense_) were seen mating in July, 1969.

All specimens of _K. alamosae_ of which I am aware were collected during the months of July or August concurrent with the Summer rainy season. J. M. Legler (unpublished field notes) collected _K. integrum_ but not _alamosae_ in the mainstream of the Río Cuchujaque (Río Fuerte drainage) 14.5 km SE of Alamos in January, 1959. Legler (pers. comm.) found conditions near Alamos to be extremely dry on 19-26 May 1978. Surface water was restricted to impoundments and rivers. Eighty specimens of K. integrum were collected in a 10 x 10 m impoundment on a small arroyo, but no K. alamosae were seen. No K. alamosae were collected from the Río Cuchujaque, from a man-made well, or from either of two cattle watering impoundments nearby.

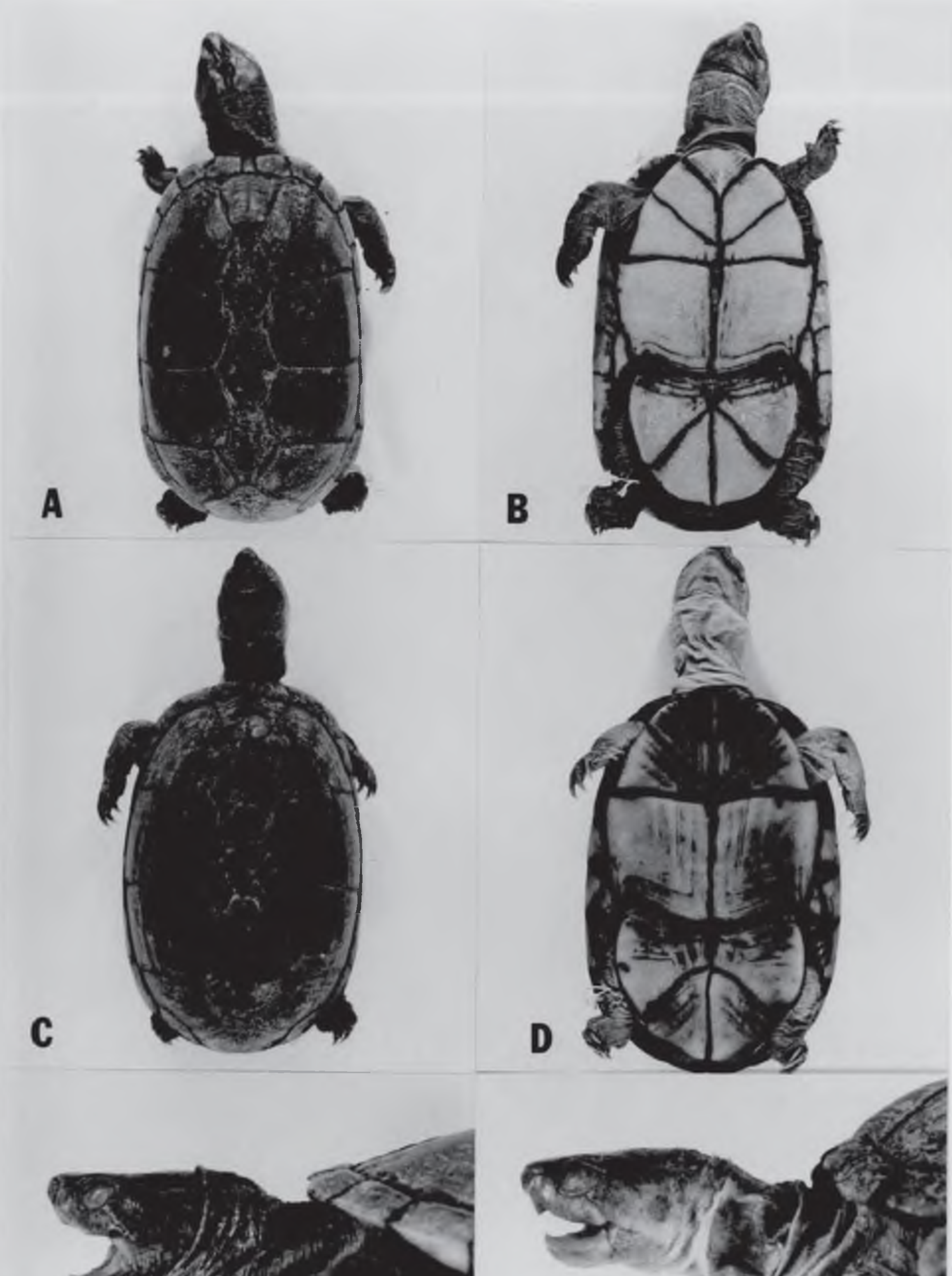
Remarks

Several collections of Kinosternon from Sonora, México reported in the literature contain specimens of K. alamosae. Of the specimens listed by Bogert and Oliver (1945) and Zweifel and Norris (1955), specimens AMNH 64163-68 and MVZ 50907-10 (Alamos, Sonora) are K. alamosae although they were identified as K. integrum by the authors. Specimens AMNH 63755-58 and MVZ 50889-902 (Guiricoba, Sonora) were correctly identified as K. integrum. A shell lacking soft parts from 23.7 km S Empalme, Sonora (UIMNH 24456) identified as K. integrum by Langebartel and Smith (1954) is tentatively identified as K. alamosae based on scute seam proportions.

Heringhi (1969) reported Kinosternon integrum and K. hirtipes from the vicinity of Alamos, Sonora. Heringhi's "hirtipes" are actually K. alamosae. K. hirtipes is not known from southern Sonora.

I consider Kinosternon alamosae to be a species most closely related to but specifically distinct from K. integrum. The two species are sympatric near Alamos, Sonora, México, but there is no evidence of morphological intermediacy which might imply subspecific intergradation or hybridization.

Figure 27. Dorsal, ventral, and head views of Kinosternon alamosae male paratype (A-B, E: ASU 6547, CL = 122 mm; 12.9 km S Alamos, Sonora, México), and female holotype (C-D, F: ASU 6383, CL = 122 mm; Rancho Carrizál, 11.3 km W Alamos, Sonora, México). Head views X.56.


A
B
C
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F

Kinosternon oaxacae Berry and Iverson

(Fig. 28)

Kinosternon oaxacae Berry and Iverson, MS. Type locality: 7.2 mi (11.2 km) N Pochutla, Oaxaca, México.

Diagnosis

Kinosternon oaxacae attains large adult body size (males to 159 mm CL, females to 130 mm CL). Most closely resembling K. integrum, it can be distinguished from all other Kinosternon by the following combination of characters in adults: (1) carapace depressed, strongly tricarinate (DKL = 3.33; DKC = 3.50); (2) plastron small, does not completely close ventral openings of shell (plastral index = ♂♂ .68/.59, ♀♀ .68/.60); (3) posterior plastral lobe with a distinct anal notch, more emarginate in males than in females; (4) inguinal and axillary scutes in contact, inguinals in contact with M5; and (5) first central scute in contact with M2.

Description

Carapace depressed (SHT = ♂♂ .34, ♀♀ .36) and wide (CWA = ♂♂ .60, ♀♀ .63; CWP = ♂♂ .63, ♀♀ .66). Carapace with three prominent keels. Central scutes each bearing a distinct posterior notch at midline. C1 usually (83% of individuals) contacts M2.

Plastron small, does not completely close ventral openings of shell; smaller in males thanin females (AHW = ♂♂ .41, ♀♀ .43; TFW = ♂♂ .37, ♀♀ .40). Plastron concave in males, flat in females. Posterior plastral hinge curved posteriorly. Posterior lobe slightly constricted at hinge (Fig. 28). Anal notch distinct, more emarginate in males than females. Axillary and inguinal scutes in contact; axillaries extend from mid-M4 to posterior M5 or anterior M6; inguinals extend from posterior M5 or anterior M6 to anterior or mid-M7 (posterior portion of inguinals tending to be replaced by skin in older, larger individuals). Interlaminal seams at the midline: ♂♂ = .15-.10-.04-.26-.09-.19; ♀♀ = .17-.08-.05-.25-.10-.21.

Dorsal head shield V-shaped or bell-shaped. Maxillary sheath strongly hooked in large males, weakly hooked in females and smaller specimens. Three to four pairs of gular barbels present; anteriormost pair (nearest mandibular symphysis) largest, remaining subequal in length. Clasping organs lacking.

Color and pattern

Ground color of carapace brown to black, or mottled combinations of brown and black. Interlaminal seams dark brown to black in paler specimens. Plastral ground color yellow to brown, interlaminal seams dark brown or black.

Dorsal ground pattern of head dark brown or gray with mottling or spotting of pale gray or cream. Ventral ground pattern of head cream to yellow with pale gray spots, more nearly immaculate in females. Dorsal and ventral patterns integrate laterally in a reticulated network (Fig. 28). Dark pigment may coalesce to form indistinct light or dark head stripes, but no well-defined head stripes are present. Jaw sheaths cream to yellow, heavily streaked with dark brown or black in males, faintly streaked or immaculate in females.

Skin of limbs dark brown or gray with darker spots dorsally, immaculate cream to gray ventrally. Tails in both sexes uniformly brown or gray dorsally and ventrally.

Geographic range

Kinosternon oaxacae is known only from the Rios Tonameca and Colotepec in southern Oaxaca, México. This region is an isolated portion of Pacific Coastal Plain limited to the north by the Sierra Madre del Sur, and to the south by the Pacific Ocean.

Natural history

The natural history of Kinosternon oaxacae is mostly unknown. It is active during mid-Summer (July and August) when all known specimens were collected. R. Conant (pers. comm.) collected the female allotype (AMNH 88884, 7 mi N Pochutla, Oaxaca) crossing a dirt road during a heavy rainstorm on 12 August 1962. It is assumed the habits of K. oaxacae are similar to those of K. integrum on the southern Pacific Coast.

Remarks

Kinosternon oaxacae is quite similar to K. integrum and is probably a fairly recent derivative of southern Pacific Coast integrum. The Sierra Madre del Sur is in close proximity to the Pacific Ocean and forms a cul-de-sac of the narrow coast between the Río Verde (the eastern limit of the range of K. integrum) and the Río Tehuantepec (the western limit of the range of K. scorpioides). It seems likely that integrum-like populations of Kinosternon became isolated in this area where the lack of gene flow and slightly different selective pressures promoted differentiation. I regard K. oaxacae as a "sibling species" (Mayr, 1969) of K. integrum.

Figure 28. Dorsal, ventral, and head views of Kinosternon oaxacae male holotype (A-B, E: UC 48857, CL = 159 mm; 7.2 mi N Pochutla, Oaxaca, México), and female allotype (C-D, F: AMNH 88884, CL = 130 mm; 7 mi N Pochutla, Oaxaca, México). Head views X.54.

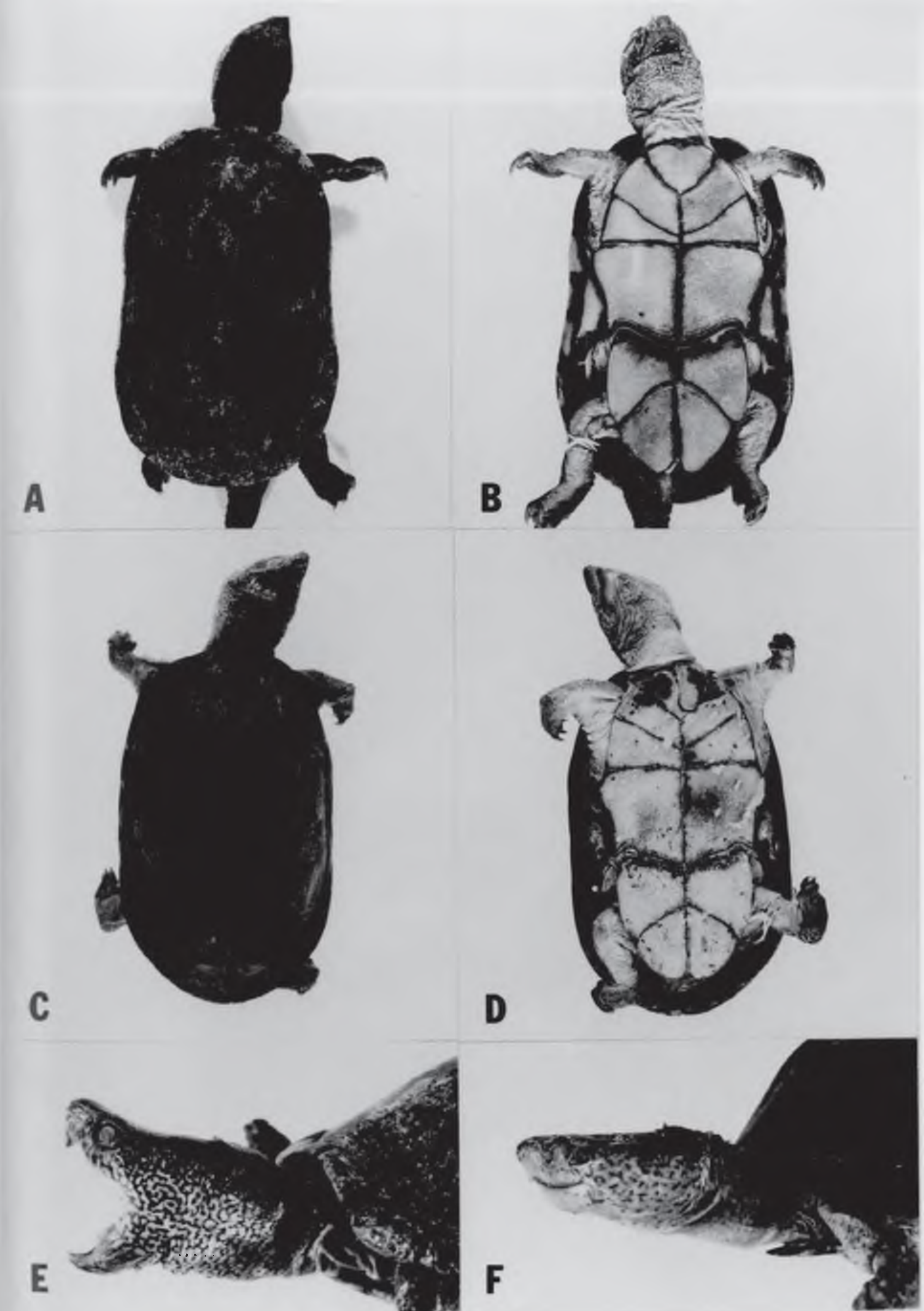
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Table 42. Characters useful in distinguishing *Kinosternon integrum*, *K. alamosae*, and *K. oaxacae*. Values are expressed as a mean (above) and range (below) of each character as a proportion of CL.

	CWA	CWP	SHT	AHW	TFW	BRL	GUL	ABL	ANL
MALES									
K. integrum	.61	.63	.36	.47	.43	.24	.16	.26	.22
	.55-.69	.56-.70	.30-.45	.39-.55	.34-.49	.18-.27	.13-.23	.20-.30	.17-.27
K. alamosae	.61	.63	.35	.48	.44	.28	.16	.29	.23
	.57-.65	.59-.68	.33-.38	.44-.52	.42-.47	.23-.32	.13-.19	.26-.32	.19-.27
K. oaxacae	.60	.63	.34	.41	.37	.24	.17	.26	.19
	.59-.62	.61-.65	.32-.36	.40-.42	.37	.21-.27	.15-.19	.24-.27	.18-.20
FEMALES									
K. integrum	.63	.66	.39	.49	.46	.26	.16	.28	.25
	.57-.73	.59-.72	.31-.46	.43-.57	.42-.50	.21-.30	.13-.24	.24-.33	.20-.29
K. alamosae	.63	.65	.41	.50	.48	.30	.16	.32	.26
	.59-.67	.60-.70	.36-.45	.47-.53	.44-.51	.28-.32	.13-.19	.28-.35	.22-.30
K. oaxacae	.63	.66	.36	.43	.40	.23	.16	.26	.21
	.60-.68	.62-.72	.36-.37	.42-.45	.39-.41	.21-.25	.15-.16	.26	.19-.22

Kinosternon scorpioides (Linnaeus) (Figs. 29-32)

Testudo scorpioides Linnaeus 1766:352. Type locality, "Surinam".
Gmelin 1789:1041.

Testudo tricarinata Schoepff 1792:Table 2. Type locality unknown.

Testudo retzii Daudin 1802:174. Type locality unknown.

Kinosternon shawianum Bell 1825:302. Type locality unknown.

Emys (Kinosternon) scorpioides Griffith 1831:13.

Kinosternon scorpioides Gray 1831:34; 1844:32; Mertens and Wermuth 1955:337; Wermuth and Mertens 1961:23; Pritchard 1967:37.

Cinosternon scorpioides Fitzinger 1835:125.

Swanka scorpioides Gray 1869:181; 1870:67.

Kinosternum scorpioides Müller 1878:644.

Cinosternum scorpioides Boulenger 1889:41.

Diagnosis

Kinosternon scorpioides is a medium to large Kinosternon which can be distinguished from all other members of the genus by the following combination of characters: (1) clasping organs lacking from posterior thigh and leg; (2) carapace moderately to strongly tricarinate in all but the oldest, largest individuals; (3) central scutes 1-4 bearing a distinct posterior notch at the midline in all but the oldest, largest individuals; (4) plastron intermediate to large, may or may not completely close the ventral openings of the shell; (5) anal scute long (ANL more than twice FEL); and (6) head intermediate to large in size.

Description

Carapace elongate to ovoid in dorsal aspect, width at M5 nearly as great as width at M8 (CWA = ♂♂ .62, ♀♀ .65; CWP = ♂♂ .63, ♀♀ .64). Widest point on carapace averages marginal 6.19 in males, 6.13 in females. Carapace with three intermediate to strong keels (DKL = 2.79; DKC = 2.46), present in all but the oldest, largest individuals. Central scutes 1-4 with distinct posterior notches at the midline in all but the oldest, largest individuals. M11 usually (73% of individuals) lower than M10, especially in larger (CL 130 mm) individuals.

Plastron variable in extent, may or may not completely close ventral openings of the shell; plastron smaller in males than in females within a population. Anal notch proportionately larger in males than females when present. Bridge variable, (BRL = .27) lacking longitudinal grooves. Interanal seam long (ANL = ♂♂ .29, ♀♀ .31). Interpectoral seam short (PEL = .03). Plastron concave in males, flat to convex in females.

Dorsal head shield rhomboidal, bell-shaped, triangular, rarely V-shaped. Maxillary sheath weakly to very strongly hooked, more strongly hooked in large males than females or subadult specimens. Three to four pairs of gular barbels present, anteriormost pair (nearest mandibular symphysis) largest, remaining pairs subequal in length. Clasping organs lacking from posterior thigh and leg.

Color and pattern

Color and pattern variable. Ground color of carapace dull brown, olive, or black, or any shade between or mottled combination; most common ground color is medium to dark brown. In pale colored specimens, interlaminal seams dark brown or black. Ground color of plastron may be gray, brown, or black with darker seams.

Head pattern variable, consisting of brown, black, or gray background, with reticulated or spotted pattern of white, cream, yellow orange, pink, or red. Ventral head pattern of pale gray, cream, or yellow; with darker spots or mottling, or immaculate. Jaw sheaths cream to yellow with darker vertical streaks, less prominent in small individuals and females than in large males. Skin of other soft parts dark gray or brown above, usually with many fine small, darker spots; and cream, light gray, or brown beneath, frequently with smaller dark spots.

Iris in living specimens dark orange (darker in males) with ruptive stellate pattern of melanin deposit around pupil.

Geographic range

The geographical range of Kinosternon scorpioides is shown in Figs. 4-6. In eastern Mexico, it is known from as far north as the Río Soto la Marina. With several gaps, it occurs southward and eastward throughout eastern México, the Yucatan Peninsula, to Guatemala and Belize in Atlantic drainages. It is apparently absent from Caribbean drainages in southern Belize, Guatemala, and most of Honduras, but occurs in Caribbean drainages of the Mosquito Lowlands in extreme eastern Honduras and Nicaragua. On the Pacific Coast, scorpioides occurs almost continuously from the Río Tehuantepec basin in southern Mexico, to the Isthmus of Panamá. K. scorpioides occurs in Atlantic drainages in northern South America from the Río Magdalena in Colombia, to the mouth and headwaters of the Amazon, and probably to the Río Sao Francisco. In southern South America, it occurs at least in the Río Paraná basin draining much of the land mass of the southern portion of the continent. Additional details of the range of _K. scorpioides_ will be given in the accounts of the subspecies.

Natural history

Kinosternon scorpioides occurs in a variety of aquatic and semi-aquatic habitats throughout its range. In areas of permanent water, its habits are similar to those of _K. integrum_; i.e., streams, swamps, and ditches in shallow, slow-moving water. However, _scorpioides_ from Central America and Mexico have a decided propensity for terrestriality. As was demonstrated earlier in this report, the wide, highly domed shell, and plastron which completely closes the ventral opening of the shell, are probably adaptations to periods of terrestrial movement associated with seasonal aquatic habitats. Teska (1976) has noted the ability of _K. scorpioides_ in Costa Rica to tolerate prolonged periods of terrestrial activity. In the Mosquito Lowlands of Nicaragua, natives collect _K. scorpioides_ during periods of estivation by burning the sedge of the pine savannahs which forces the turtles from their refugia, or by probing areas of drying mud for buried specimens (J. M. Legler, E. O. Moll, unpublished field notes).

On Isla Cozumél, Mexico Duellman (1965) found specimens of _scorpioides_ "buried in mud or dug in at the bases of clumps of cat-tails in a partly dried up marsh." Meyer and Wilson (1973) stated _scorpioides_ in Honduras occurred "in streams and ponds in the daytime and at night" and on roads during rains, in Tropical Moist Forest, Tropical Dry Forest, and Subtropical Wet Forest formations from sea level to 750 m elevation. Hartweg and Oliver (1940) found scorpioides abundant in a "very filthy watering hole" near Tehuantepec, México. Medem (1960) reported it inhabits streams, small pools, lakes, swamps, and ponds in South America.

Remarks

The results of the phenetic analyses in this study suggest that *Kinosternon scorpioides* consists of four subspecies in México and Central America: (1) *K. s. cruentatum* in Mexico, Belize and Guatemala (populations 21-23 and 25-31); (2) *K. s. abaxillare* in the Río Grande de Chiapas, México (population 24); (3) *K. s. albogulare* which occupies most of Central America on the Pacific Coast from Honduras to southern Costa Rica (populations 34-37; populations 32-33 are intermediate between *K. s. cruentatum* and *K. s. albogulare*), and in Caribbean drainages along the Mosquito Coast from eastern Honduras to central Nicaragua (populations 42-44); and *K. s. scorpioides* which occurs in Central America only at the Isthmus of Panama (populations 40 and 45), although populations from western Panamá and adjacent Costa Rica (38-39) are intermediate between *K. s. scorpioides* and *K. s. albogulare*.

As noted under "Remarks" under *K. integrum*, I feel that the evidence suggests that *K. scorpioides* and *K. integrum* are closely related but specifically distinct.

Kinosternon scorpioides cruentatum Dumeril, Bibron
and Dumeril (Fig. 29)

Cinosternon cruentatum Dumeril, Bibron and Dumeril 1851:16. Type locality: restricted by Smith and Taylor (1950b) to San Mateo del Mar, Oaxaca, Mexico.

Kinosternum mexicanum LeConte 1854:182. Type locality unknown.

Kinosternum cruentatum Troschel 1855:415.

Kinosternon triliratum LeConte 1859:6. Type locality unknown.

Cinosternon triliratum Strauch 1862:41.

Cinosternon mexicanum Strauch 1862:41.

Cinosternum triliratum Strauch 1865:187.

Kinosternon mexicanum Müller 1865:598.

Cinosternum shavianum Cope 1866:123.

Swanka mexicana Gray 1870:69.

Swanka trilirata Gray 1870:69.

Cinosternum shawianum Bocourt 1876:387.

Kinosternon cruentatum Müller 1878:750; Wettstein 1934:14; Stuart 1935:8; 1948:44; Hartweg and Oliver 1940:13; Mertens and Wermuth 1955:335; Alvarez del Toro 1960:44; 1973:18; Wermuth and Mertens 1961:14; Duellman 1965:591; Neill 1965:119; Casas Andreu 1967:38; Pritchard 1967:44.

Ciniosternum shawianum Sumichrast 1880:169.

Kinosternon shawianum Sumichrast 1881-1882:270.

Cinosternum shawianum Sumichrast 1882:34.

Cinosternum cruentatum Cope 1887:22; Boulenger 1889:

Cinosternum shawanianum Velasco 1892:79.

Kinosternon cruentatum cruentatum Schmidt 1941:488; Schmidt and Shannon 1947:69; Smith and Taylor 1950a:23; Mertens and Wermuth 1955:335; Wermuth and Mertens 1961:16; Stuart 1963:48; Casas

Andreu 1965:381, 385; Pritchard 1967:44.

Kinosternon cruentatum consors Stejneger 1941:458. Type locality: Cozumel Island: Yucatán (Quintana Roo): México. Placed in synonymy with K. cruentatum Dumeril, Bibron, and Dumeril by Duellman 1965:591. Smith and Taylor 1950a:24; Mertens and Wermuth 1955:335; Wermuth and Mertens 1961:16; Casas Andreu 1965:381, 385; Pritchard 1967:44.

Kinosternon crenulatum Pearse 1945:222.

Kinosternon scorpioides Legler 1965:621; Iverson 1976:258.

Kinosternun cruentatum cruentatum Álvarez del Toro 1973:165.

Diagnosis

Kinosternon scorpioides cruentatum attains smallest adult body size of any K. scorpioides subspecies (males to 151 mm CL, females to 138 mm CL), and can be distinguished from other subspecies of K. scorpioides by the following combination of characters in adults: (1) carapace wide, highly domed (Table 43); (2) carapace strongly tricarinate in all but the oldest, largest individuals (DKL = 2.95, DKC = 2.79); (3) interabdominal seam short, interlaminal seams of plastron at midline: ♂♂ = .12-.14-.02-.26-.05-.31, ♀♀ = .16-.14-.02-.28-.04-.32; (4) plastron extensive, completely closing ventral openings of shell (Table 43; plastral index = .78/.75 ♂♂, .77/.74 ♀♀); (5) posterior plastral hinge a straight line perpendicular to midline (Fig. 29); (6) axillary and inguinal scutes rarely (7% of individuals) in contact (AIC = .140); (7) anal notch small or lacking; (8) head of intermediate size in most populations (HW = ♂♂ .21, ♀♀ .19 from populations 21-23, 25-30), larger in specimens from Belize (HW = ♂♂.23,

♀♀.22 from population 31); and (9) head pattern marbled or speckled red, orange, yellow, or cream on slate gray or black background (Fig. 29 E-F).

Color and pattern

Color and pattern of carapace and plastron as noted under K. scorpioides. Ground color of head dark gray, brown, or black dorsally and laterally. A marbled or speckled pattern of pale gray, cream, yellow, orange or red laterally, sometimes forming ragged lateral stripes (Fig. 29). A pale postorbital stripe usually extending from posterior orbit to angle of jaws. Ventral ground color of head gray, brown, or black with pale gray or cream spots or blotches.

Juvenile head pattern essentially as in adults, but ground color paler and lateral flecks and stripes more prominent and more brightly colored. Developmental pattern is one of gradual deposition of melanin resulting in general darkening and obscuring of pattern.

Head pattern geographically variable. Background color slate gray to black with bright red or orange mottling in southern Mexican populations (21-23). Background color gray with yellow flecks in populations from the Yucatan Peninsula (28-30). Hartweg (in Hartweg and Oliver, 1940) reported blood red bands behind the eyes in specimens from Tehuantepec, México, and yellow bands in specimens from Quintana Roo, México.

Geographic range

K. s. cruentatum is known from the Gulf Coastal Lowlands of eastern Mexico from the Río Soto la Marina southward, the Yucatan

Peninsula and Isla Cozumel, and the Soconusco Coast of southern Mexico and Guatemala (populations 21-23, 25-31).

In eastern Mexico, *K. s. cruentatum* has been collected as far north as the Río Soto La Marina basin coastal Tamaulipas, México (Nelson and Nickerson, 1966). Specimens are known from throughout the Río Pánuco basin below elevations of 300 m (above which it is replaced by *K. integrum*; *cf*. Iverson and Berry, MS), but there are no records between the Río Pánuco and the Sierra Volcánica Transversal 70 km NW of Veracruz, Veracruz (whether this lack of specimens represents a real gap in the range or simply inadequate collecting is not known). *K. s. cruentatum* is known from several localities between the Sierra Volcánica Transversal and the Río Papaloapan basin (in which it is, once again, replaced by *K. integrum* at higher elevations). A second gap in the range exists between the Río Papaloapan and the Río Usamacinta basin (*K. s. abaxillare* occupies the Río Grande de Chiapas in the upper Río Grijalva). The range includes much of the eastern and northern Yucatan Peninsula, the Guatemalan Highlands, and Belize.

On the Pacific Coast, *K. s. cruentatum* occurs from the Río Tehuantepec basin in Oaxaca, México, along the Soconusco Coast of southeastern México and Guatemala. Near the Río Lempa basin of El Salvador, Guatemala, and Honduras *K. s. cruentatum* intergrades with *K. s. albogulare*.

Specific localities for *K. s. cruentatum* are given by Bocourt (1876; as *C. shawianum* and *C. cruentatum*); Boulenger (1889); Casas Andreu (1965, 1967); Cochran (1961); Cope (1887); Davis (1953); Dixon, Ketchersid, and Lieb (1972); Duellman (1965); Duges (1894, 1896);

Gaige (1936); Greene (1972); Hartweg and Oliver (1940); Langebartel (1953); Mertens (1952); Müller (1878); Neill (1965); Nelson and Nickerson (1966); Smith and Taylor (1950b); Stejneger (1941); Strauch (1862, 1965); Stuart (1963); Sumichrast (1880; 1881-1882; as *C. shawianum*); Taylor (1952); Wettstein (1934); and Williams and Wilson (1966).

The six specimens from "La Majada, near Apatzingan", Michoacán, México reported by Schmidt and Shannon (1947) were correctly referred to *K. integrum* by Smith and Taylor (1950b).

Remarks

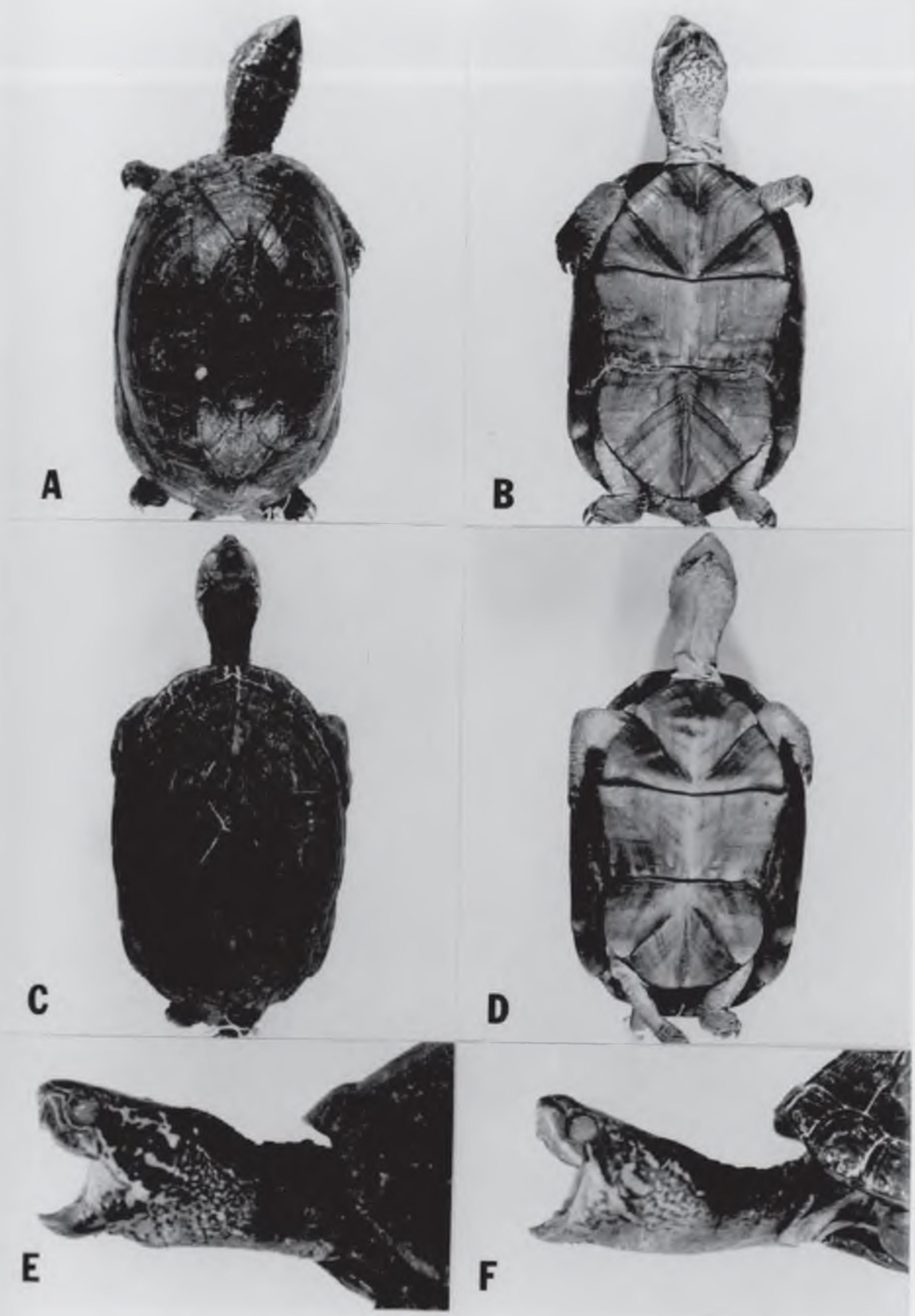
Legler (1965) placed *Kinosternon cruentatum* in synonymy with *K. scorpioides*, an arrangement followed subsequently by Iverson (1976). The results of the analyses in the present study strongly support their conclusions. The presence of intergrade populations (32-33) intermediate geographically as well as phenetically between *K. s. cruentatum* and *K. s. albogulare* to the south is, in itself, convincing evidence of the propriety of this arrangement.

Stejneger (1941) described *K. cruentatum consors* from Isla Cozumel and the extreme northeastern portion of the Yucatan Peninsula, which was said to differ from the nominal subspecies in "shell averaging narrower and lower; front lobe of plastron averaging shorter and 'midlobe' (the fixed part) longer." Duellman (1965) reassessed the status of *K. cruentatum consors* using specimens from Isla Cozumel (10 specimens) and various mainland populations (13 specimens) and concluded that of Stejneger's diagnostic characters, only the width of the shell showed significant difference in the Cozumel specimens.

Duellman (1965) stated "the absence of characters to distinguish the specimens from Isla Cozumel and the northern part of the Yucatan Peninsula from individualsfrom the rest of the range of the species makes it necessary to place the name Kinosternon cruentatum consors Stejneger 1941 ... as a synonym of K. cruentatum Dumeril and Bibron, 1851". However, Duellman's synonymy was subsequently ignored by Pritchard (1967) who discussed K. cruentatum consors.

The present study is based on a vastly greater number of specimens than any before, and presents an excellent opportunity to test the premise that Isla Cozumel and Yucatan populations (29-30) differ in the above characters from mainland populations (21-23, 25-28, and 31). The values for each character as a proportion of CL, and averaged for Cozumel and northeastern Yucatan (first) and mainland populations (second) follow: CWA = .63, .65; CWP = .62, .65; SHT = .43, .45; GUL + HUL + PEL (= anterior lobe length) = .31, .33; and ABL = .28, .27. That is, the trends noted by Stejneger (1941) prove to be consistent, although I must agree with Duellman (1965) that the differences are not sufficient to warrant taxonomic distinction for the Cozumel and Yucatan populations. Furthermore, the canonical and distance analyses presented earlier demonstrated little tendency for populations 29 and 30 to be significantly phenetically discrete. The evidence suggests that Duellman (1965) was correct in placing the name cruentatum consors in synonymy with cruentatum (= K. scorpioides cruentatum).

Figure 29. Dorsal, ventral, and head views of Kinosternon scorpioides cruentatum male (A-B, E: UU 7631, CL=116 mm), and female (C-D, F: UU 7633, CL=103 mm, both from vicinity of Tonalá, Chiapas, México). Head views X .54.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Kinosternon scorpioides abaxillare Baur

(Fig. 30)

Kinosternon abaxillare Baur *in* Stejneger, 1925:462. Type locality: Tuxtla, Chiapas, México. Smith and Taylor, 1950a:22; Mertens and Wermuth, 1955:334; Alvarez del Toro, 1960:45; 1973:20; Wermuth and Mertens, 1961:10; Casas Andreu, 1965:385; 1967:34; Pritchard, 1967:44.

Kinosternun abaxillare Alvarex del Toro, 1973:195.

Diagnosis

Kinosternon scorpioides abaxillare attains relatively small adult body size (males to 150 mm CL, females to 155 mm CL), and can be distinguished from all other subspecies of *Kinosternon scorpioides* by the following combination of characters in adults: (1) carapace wide, intermediate in height (Table 43); (2) carapace strongly tricarinate in all but the oldest, largest individuals (DKL = 2.77; DKC = 2.94); (3) interabdominal seam long, interlaminal seams of plastron at midline: ♂♂ = .17-.11-.03-.31-.03-.30, ♀♀ = .17-.10-.04-.33-.03-.30; (4) plastron extensive, completely closing ventral openings of the shell (Table 43; plastral index = ♂♂ .79/.74, ♀♀ .78/.75); (5) posterior plastral hinge curved posteriorly (Fig. 30); (6) axillary scutes absent, or axillary-abdominal seam incomplete (Fig. 30); (7) anal notch small or lacking; (8) head small (HW = ,19); (9) head pattern of pale gray to yellow marbling and dots on olive to slate background (see Alvarex del Toro, 1973).

Color and pattern

Color and pattern of carapace and plastron as noted under *K. scorpioides* above. ground color of head gray or olive with marbled or spotted pattern of pale gray, cream, or yellow laterally (see Alvarez del Toro, 1973). Head pale gray ventrally with numerous darker gray spots.

Juvenile pattern essentially as above, but ground color paler, marbling more prominent. Developmental pattern involves gradual deposition of melanin causing gradual obscuring and darkening of pattern.

Geographic range

K. s. abaxillare is known only from the Río Grande de Chiapas and its tributaries in the Chiapas-Guatemala Depression. It apparently does not occur in the Río Mescalapa to which the Río Grande de Chiapas is tributary,or anywhere else in the Río Grijalva basin.

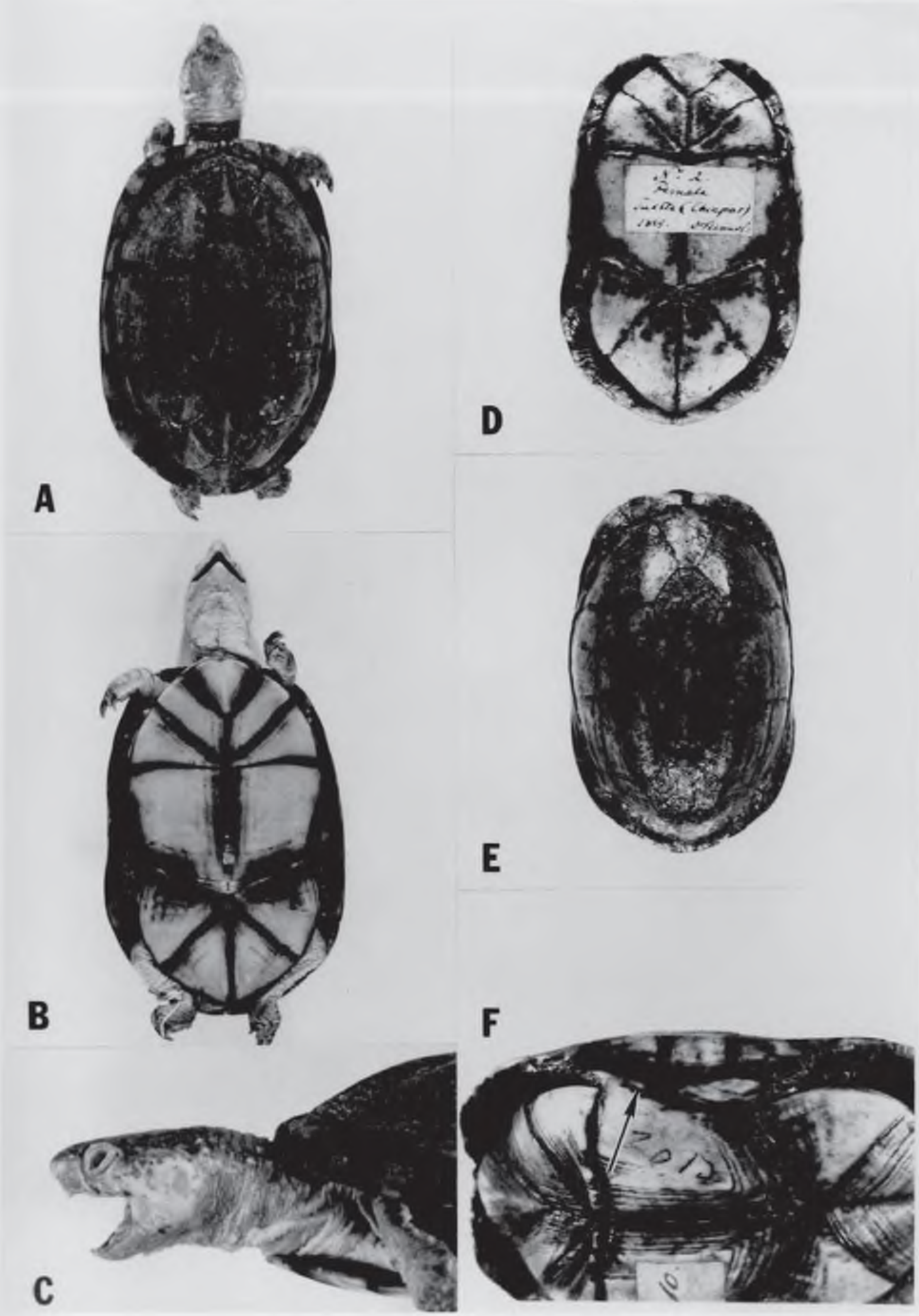
Specific localities for *K. s. abaxillare* are listed by Greene (1972); Nelson and Nickerson (1966); and Stejneger (1925).

Remarks

This report is the first to consider *abaxillare* a subspecies of *K. scorpioides*. The results of the preceding analyses suggest that *abaxillare* is less distinctive than previous authors have suggested; in fact, the analyses indicate that *abaxillare* could conceivably be considered an intergrade population between *K. s. cruentatum* and *K. s. albogulare*. Nevertheless, it is here suggested that *abaxillare* should be considered a subspecies of *K. scorpioides* based on the following: (1) *abaxillare* is phenetically distinct from populations of K. s. cruentatum to which it is closest geographically (although they are separated by the Sierra Madre del Sur, less than 30 km separate the two subspecies in southeastern Chiapas); (2) there is no known intermediacy (intergradation) between K. s. abaxillare and and K. s. cruentatum; (3) abaxillare is geographically isolated from populations of K. s. albogulare to the south; and (4) abaxillare is reasonably distinct phenetically from both albogulare and cruentatum.

Alvarez del Toro (1973:18) has stated that "Kinosternon cruentatum ... se encuentra en casi todo el estado (Chiapas)" (Kinosternon cruentatum occurs in almost all of the state), implying that K. s. cruentatum and K. s. abaxillare are sympatric in the Río Grande de Chiapas. Should this sympatry prove to be real, and if it can be established that there is no morphological intermediacy between cruentatum and abaxillare, then abaxillare probably should be considered a distinct species. I have seen no specimens of K. s. cruentatum from the Río Grande de Chiapas, or any evidence of intermediacy (confirmed by the statistical analyses in this study). Nevertheless, Sr. Alvarez del Toro has suggested to me quite emphatically (pers. comm.) that both species were once common in the Río Sabinal at Tuxtla Gutierrez (the type locality of abaxillare) but that pollution has extirpated all aquatic life in the river. By his own admission Sr. Alvarez del Toro has worked relatively little with the turtles in the area. I submit that the "cruentatum" seen in the Central Depression of Chiapas were simply abaxillare in which axillary scutes are some times present, or K. s. cruentatum imported from the nearby Pacific Coast. Only one Kinosternon, K. s. abaxillare,

Figure 30. Dorsal, ventral, and head views of _Kinosternon scorpioides abaxillare_ subadult male (A-C: UU 12423, CL=112 mm), shell of female paratype (D-E: USNM 7519, CL=122 mm), and shell of subadult male paratype showing presence of partial axillary-abdominal seam at arrows tip (F: USNM 7527, CL=113 mm, all specimens from Tuxtla Gutiérrez, Chiapas, México). Head view X .56.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occurs in the Río Grande de Chiapas.

Axillary scutes are frequently absent in specimens of K. s. cruentatum and K. s. albogulare as well as in most K. s. abaxillare. These scutes are lost by two distinctive processes. In some specimens of abaxillare there is an incomplete seam separating the axillary from the abdominal scute, suggesting the axillary has partially fused with the abdominal (as in USNM 7527, a juvenile paratype of K. abaxillare; Fig. 30). The axillary is frequently vestigial in the other two subspecies, and is pushed forward of the bridge until it is occasionally lost entirely. The functional significance of axillary scute reduction or loss is not clear, but it occurs in populations of Kinosternon with extensive, highly kinetic plastrons. Axillary reduction may be associated with structural strengthening of the bridge section, or increasing mobility of the relatively wide anterior lobe. K. alamosae is another species with a relatively wide anterior lobe, and it has reduced axillary scutes as well

Kinosternon scorpioides albogulare Dumeril and Bocourt (Fig. 31)

Cinosternon albogulare Dumeril and Bocourt, 1870:24. Type locality: San Jose, Costa Rica. Gray, 1873:113.

Cinosternum albogulare Cope, 1875:153.

Kinosternon cruentatum Dunn and Emlen, 1932:25.

Kinosternon cruentatum albogulare Wettstein, 1934:14.

Kinosternon scorpioides albogulare Dunn and Saxe, 1950:145; Mertens and Wermuth, 1955:337; Wermuth and Mertens, 1961:25; Pritchard, 1967:37.

Diagnosis

Kinosternon scorpioides albogulare attains the largest adult size of any K. scorpioides (males to 205 mm CL, females to 174 mm CL) and can be distinguished from the other subspecies of K. scorpioides by the following combination of characters in adults: (1) carapace wide, highly domed (Table 43); (2) carapace strongly or intermediately tricarinate in all but the oldest, largest individuals (DKL = 2.72, DKC = 2.31); (3) interabdominal seam of intermediate length, interlaminal seams of the plastron at the midline: ♂♂ = .16-.14-.02-.28-.03-.29, ♀♀ = .17-.15-.02-.30-.03-.31; (4) plastron extensive, completely closing ventral openings of shell (Table 43; plastral index = ♂♂ .79/.75; ♀♀ .79/.77); (5) posterior plastral hinge curved posteriorly (Fig. 31); (6) axillary and inguinal scutes usually (86% of individuals) in contact (AIC = 1.73); (7) anal notch small or lacking; (8) head pattern consisting of broken series of spots and reticulation of pink, orange, yellow, or cream on a dark gray to brown background.

Color and pattern

Color and pattern of carapace and plastron as noted under K. scorpioides above. Ground color of head slate gray to brown dorsally and laterally. Pattern of spots or reticulation of pink, orange, yellow, or cream laterally; spots frequently fusing to form a series of horizontal stripes (Fig. 31). Ventral ground color of head pale gray or cream with dark spots; rarely immaculate.

Juvenile pattern consists of marbled pattern of pale yellow to pink on gray or light brown ground color. Gradually replaced by darker reticulate pattern in subadults, and pattern of spots in adults. Ontogenetic pattern consists of gradual fragmentation of juvenile marbled pattern; melanin deposition gradually darkens and obscures juvenile pattern.

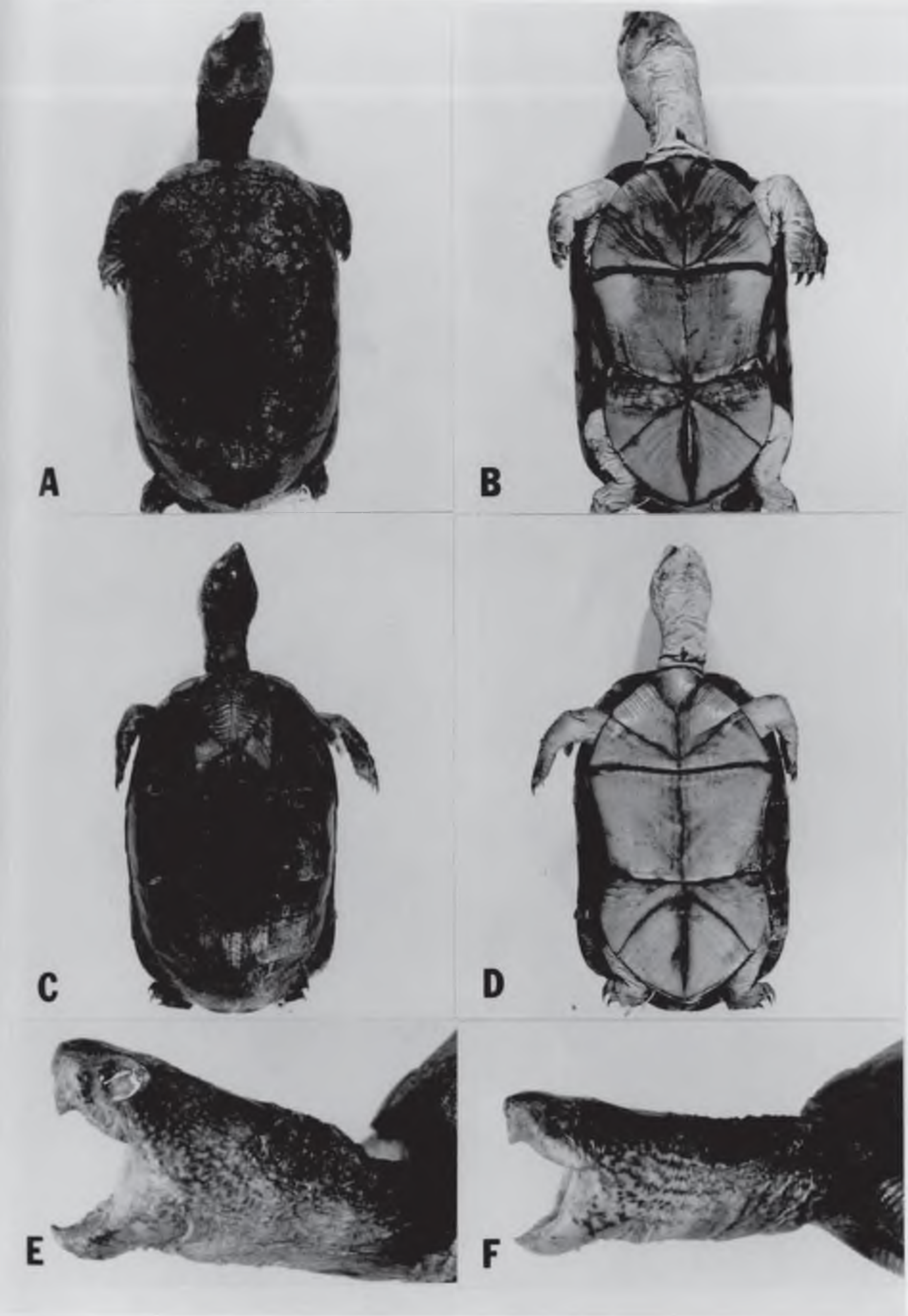
Geographic range

The geographic range of *K. scorpioides albogulare* includes virtually every Pacific drainagefrom the Golfo de Fonseca, Honduras, to those into Bahia de Coronada and the Nicoya Peninsula in southern Costa Rica. It occurs in Caribbean drainages of the northeastern Honduran and Nicaraguan Mosquito Lowlands, and the Nicaragua Depression including drainages into Lagos de Managua and Nicaragua, and San Andres Island, Colombia. This includes populations 34-37, and 42-44.

To the north, *K. s. albogulare* intergrades with *K. s. cruentatum* in the vicinity of the Río Lempa (Pacific) and its tributaries in Guatemala, El Salvador, and Honduras (populations 32-33 are phenetically as well as geographically intermediate). *K. s. albogulare* intergrades with *K. s. scorpioides* along the Pacific Coast to the south, including all drainages of the Peninsula de Osa southward (but not including) the Peninsula de Azuero and Isla de Coiba (populations 38-39).

Specific localities for *K. s. albogulare* are listed by Dumeril and Bocourt (1870), Dunn (1945a), Dunn and Emlen (1932), Dunn and Saxe (1950), Mertens (1952), Meyer (1966), Meyer and Wilson (1973), Tamsitt and Valdivieso (1963), Valdivieso and Tamsitt (1963), and Wettstein (1934).

Figure 31. Dorsal, ventral, and head views of Kinosternon scorpioides albogulare male (A-B, E: UU 7220, CL=156 mm, Rancho El Morillo, Río San Juan, Nicaragua), and female (C-D, F: UU 7207, CL=148 mm, New Found Out, 15 mi NNE Bluefields, Zelaya, Nicaragua). Head views X .61 (♂) and X .56 (♀).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Kinosternon scorpioides scorpioides (Linnaeus)

(Fig. 32)

Testudo scorpioides Linnaeus, 1766:352. Type locality: Surinam. Gmelin, 1789:1041.

Kinosternon longicaudatum Spix, 1824:17. Type locality: Brazil.

Kinosternon brevicaudatum Spix, 1824:18. Type locality: Río Solimoes (= Río Amazon, Brazil).

Kinosternom longicaudatum Gray, 1825:211.

Terrapene tricarinata Gravenhorst, 1829:16. Type locality unknown.

Cinosternon scorpioides Fitzinger, 1835:125; Orbigny, 1847:6; Dumeril, 1825:238.

Thyrosternum longicaudatum Troschel, 1860:270.

Swanka scorpioides Gray, 1870:69.

Cinosternon scorpioides scorpioides Siebenrock, 1907:576.

Cinosternum scorpioides integrum forma brasiliana (nomen illegitimum) Siebenrock, 1907:579.

Kinosternon integrum Ruthven, 1922:69.

Kinosternon scorpioides scorpioides Müller and Hellmich, 1936:98; Freiberg, 1936:171; Mertens and Wermuth, 1955:337; Medem, 1960:345; Wermuth and Mertens, 1961:25; Pritchard, 1967:37; Cunha, 1970:5; Dixon and Soini, 1977:25.

Kinosternon panamensis Schmidt, 1946:5. Type locality: Panamá Railroad, Canal Zone, Panamá.

Kinosternon scorpioides panamense Mertens and Wermuth, 1955:338; Wermuth and Mertens, 1961:26; Pritchard, 1967:40.

Diagnosis

Kinosternon scorpioides scorpioides is a large subspecies (males to 178 mm CL, females to 156 mm CL), which can be distinguished from all other subspecies of *Kinosternon scorpioides* by the following combination of characters in adults: (1) carapace relatively narrow, depressed (Table 43); (2) carapace strongly tricarinate (DKL = 3.11, DKC = 3.16); (3) interabdominal seam of intermediate length, interlaminal seams of plastron at midline: ♂♂ = .15-.10-.03-.29-.09-.24, ♀♀ = .16-.10-.03-.29-.09-.24; (4) plastron intermediate to small, does not completely close ventral openings of shell (Table 43; plastral index = ♂♂ .72/.61; ♀♀ .73/.64); (5) posterior plastral hinge curved posteriorly (Fig. 32); (6) axillary scutes in contact (AIC = 1.89); (7) anal notch usually distinct, more emarginate in males than in females; and (8) head pattern consisting of yellow, pale gray, or pale brown dots or reticulation on darker brown, gray, or olive background.

Color and pattern

Color and pattern of carapace and plastron as noted under *K. scorpioides* above. Head with gray or brown ground color dorsally and laterally, bearing reticulate or spotted pattern of gray, yellow, or cream. Ventral ground color pale gray with darker spots.

In juveniles, pale spots or reticulation brighter in color, ground color paler. Entire effect is that of bolder head pattern than that of adults. Developmental pattern consists of gradual deposition of melanin resulting in overall darkening and obscuring of pattern, expecially in larger males.

Geographic range

K. s. scorpioides is known from Pacific drainages of the Peninsula de Azuero and the Isthmus of Panama in Central America (populations 40 and 45). It intergrades with *K. s. albogulare* along the Pacific Coast of Panama north of the Peninsula de Azuero to the Peninsula de Osa (populations 38-39).

The bulk of the geographic range of *K. s. scorpioides* is in South America. It is possible to delineate the geographic range in general terms even though systematic collections of *Kinosternon* from South America are lacking. An unpublished MS by F. Medem, several recent papers with locality records, and the specimens examined for this study provide the basis for such inferences. *K. s. scorpioides* occurs throughout the Río Magdalena basin in northwestern Colombia, but does not occur on the Pacific slopes of the Cordillera Occidental; it occurs in Atlantic Coastal areas more-or-less completely across the northern coast of continental South America including the island of Trinidad; near the mouth of the Amazon River, and in its headwaters near the Andes (and probably throughout its middle portion); and in mountainous eastern Brazil.

Specific localities are given by Dixon and Soini (1977), Dunn (1945b), Medem (1957, 1960), and Ruthven (1922).

Remarks

Schmidt (1946) described *Kinosternon panamensis* as the *scorpioides*-group member in the Canal Zone. Mertens and Wermuth (1955) reduced *panamensis* to a subspecies of *scorpioides*. The results of the phenetic analyses in this study suggest that *K. s.*

panamense is sufficiently phenetically similar to K. s. scorpioides to place them in the same subspecies.

Schmidt (1946) suggested K. panamensis could be distinguished from K. scorpioides by (1) the presence of less distinct carapacal keels; (2) the posterior end of the plastron is only very narrowly notched; and (3) the heads of males are less enlarged. I have examined the holotype of K. panamensis (USNM 11736) and the adult paratypes, plus a number of additional specimens from the vicinity of the type locality in the Canal Zone. Schmidt's (1946) proposed diagnostic characters for panamensis can be compared to South American scorpioides as follows: (1) DKL and DKC average 2.73 and 2.21 in panamensis, and 3.19 and 3.33 in scorpioides; (2) NOT = .015 in panamensis, and .024 in scorpioides; and (3) HW = .21 in panamensis males, and .21 in scorpioides males. There are differences in carapacal keels and depth of the anal notch between Panamanian and South American populations of scorpioides, but these differences can be explained as partial intermediacy in these characters between K. s. scorpioides and K. s. albogulare in the Panamanian specimens. There is no significant difference in head sizes.

I propose placing the name Kinosternon panamensis in synonymy with Kinosternon scorpioides scorpioides (Linnaeus) for the following reasons: (1) the diagnostic characters proposed by Schmidt (1946) are either clinal (keeling and notch depth) or non-diagnostic (head size); and (2) the phenetic analyses presented in this study indicate similarities between South American and Panamanian populations which are too great to justify the recognition of two taxa.

Figure 32. Dorsal, ventral, and head views of *Kinosternon scorpioides scorpioides* male (A-B, E: UU 7608, CL=144 mm), and female (C-D, F: UU 7610, CL=138 mm, both from 1/2 mi N Red Tank, Canal Zone). Head views X .54.

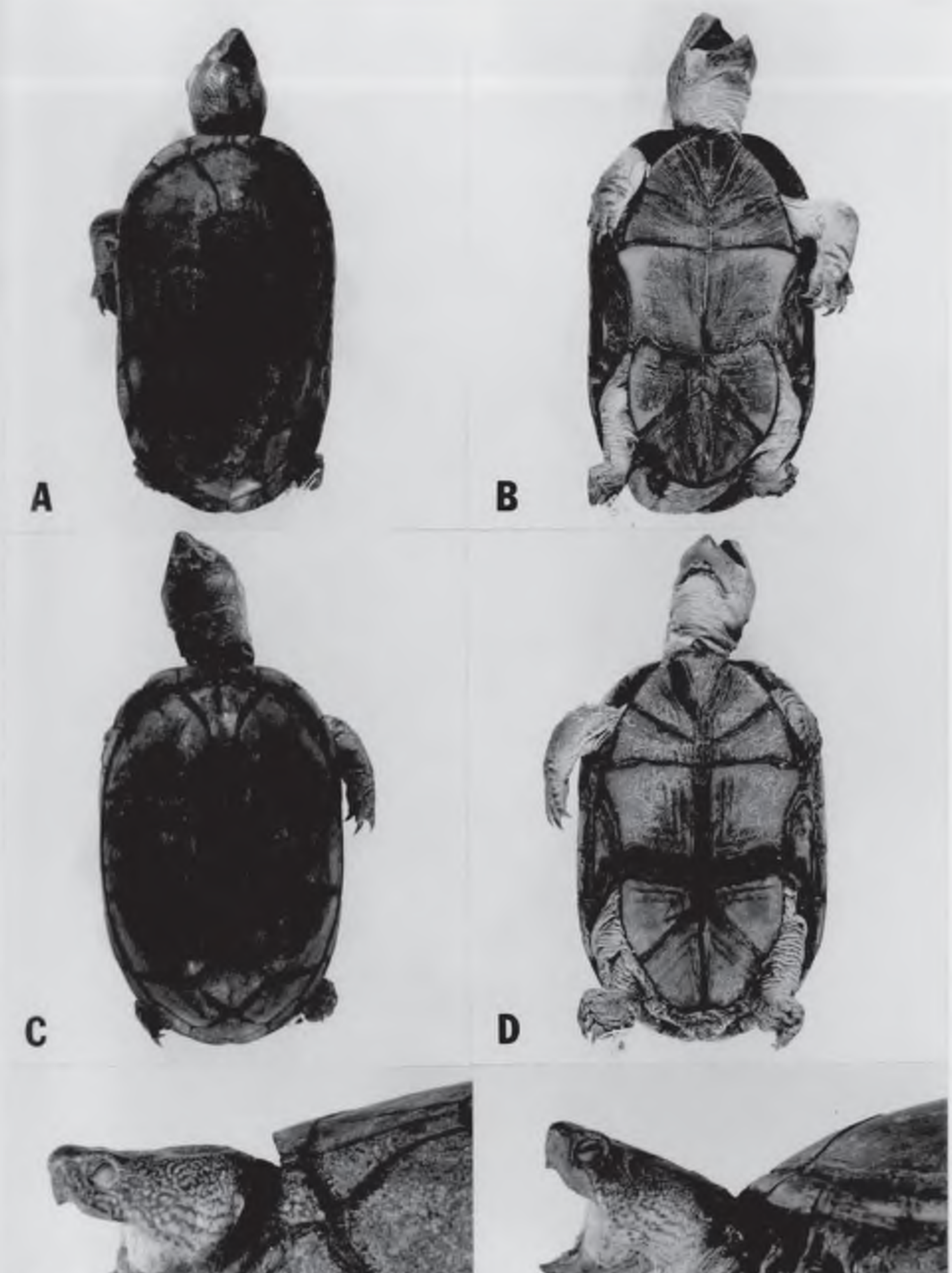
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Table 43. Characters as proportions of CL useful in distinguishing the subspecies of Kinosternon scorpioides of Mexico and Central America (means above, and range below).

	CWA	CWP	SHT	AHW	TFW	BRL	GUL	ABL	ANL
MALES									
K. s. cruentatum	.63	.63	.43	.49	.47	.29	.16	.26	.31
	.56-.71	.57-.70	.37-.56	.45-.56	.43-.51	.23-.32	.13-.19	.20-.31	.25-.34
K. s. albogulare	.63	.63	.41	.50	.47	.25	.16	.28	.29
	.56-.69	.56-.67	.38-.48	.45-.53	.41-.53	.23-.29	.13-.18	.21-.33	.25-.33
K. s. abaxillare	.62	.65	.38	.49	.48	.28	.17	.31	.30
	.59-.64	.62-.67	.36-.39	.45-.53	.44-.51	.26-.31	.14-.20	.30-.32	.28-.32
K. s. scorpioides	.60	.62	.35	.43	.38	.24	.15	.26	.22
	.56-.66	.54-.71	.32-.39	.37-.48	.32-.41	.21-.28	.12-.17	.22-.28	.16-.29
FEMALES									
K. s. cruentatum	.65	.65	.46	.50	.48	.31	.16	.28	.32
	.59-.73	.60-.71	.36-.52	.45-.56	.44-.53	.27-.34	.14-.19	.20-.34	.26-.37
K. s. albogulare	.66	.65	.46	.52	.50	.28	.17	.30	.31
	.58-.72	.59-.72	.40-.55	.46-.59	.44-.56	.24-.32	.15-.19	.24-.35	.27-.35
K. s. abaxillare	.63	.64	.39	.49	.48	.30	.17	.33	.30
	.60-.66	.61-.67	.37-.41	.46-.52	.44-.52	.29-.32	.14-.20	.31-.34	.28-.32
K. s. scorpioides	.62	.64	.38	.45	.41	.27	.16	.29	.24
	.60-.69	.57-.67	.32-.45	.36-.50	.35-.45	.23-.30	.14-.18	.25-.31	.18-.30

Comments on South American Subspecies of *Kinosternon scorpioides*

Three subspecies of *Kinosternon scorpioides* have been described from South America in addition to the nominal subspecies discussed above. These are: (1) *K. s. serei* Freiberg (1936; type locality El Tabacal, Salto, Argentina; (2) *K. s. pachyurum* Müller and Hellmich (1936; type locality Villa Montes, Bolivia); and (3) *K. s. carajasensis* Cunha (1970; type locality Serra dos Carajás, Serra Norte, Pará, Brazil).

Only specimens of *K. s. scorpioides* and *K. s. serei* were included in the phenetic analyses in this study. The analyses suggest that *K. s. serei* deserves subspecific recognition in spite of Hellmich's (1958) suggestion that it is synonymous with *K. s. scorpioides*. The names *serei* and *pachyurum* probably refer to the same taxon since (1) the descriptions and figures of *serei* and *pachyurum* are in general agreement; and (2) the type locality of *serei* is on the Río Bermejo and that of *pachyurum* is on the Río Pilcomayo, both of which are tributaries of the Río Paraná. It is suggested here that but one subspecies of *K. scorpioides* occurs in southern Bolivia and northern Argentina. The name which applies to this subspecies is *K. s. serei* which was described earlier in 1936 than was *pachyurum* (29 August *vs.* 8 October) and has priority; *i.e.*, *K. s. pachyurum* is a subjective junior synonym of *K. s. serei*.

The most recently described subspecies of *K. scorpioides* is *K. s. carajasensis* from a small mountain range, the Serra dos Carajás, in eastern Brazil. *K. s. carajasensis* is said to differ from the nominal subspecies in having a highly domed carapace in which the median keel is much more prominent than the lateral keels, a vestigial or absent nuchal scute, and a large head. It is difficult to assess the relationships between K. s. carajasensis and K. s. scorpioides without having seen specimens of the former, but I am inclined tentatively to agree that carajasensis is a valid subspecies of K. scorpioides based on Cunha's (1970) description and figures.

Kinosternon leucostomum Dumeril, Bibron, and Dumeril (Figs. 33-34)

Cinosternon leucostomum Dumeril, Bibron, and Dumeril, 1851:17. Type locality: "N. Orleans, Mexique; Río Usamasinta (Amer. centr.): Amer. septentr. ?Vallée de la Madeleine (N. Grenada)". Restricted by Schmidt (1941:48) to Río Usamacinta, Petén, Guatemala; and again restricted by Smith and Taylor (1950b:26) to Cosamaloapam, Veracruz, Mexico. Dumeril and Dumeril, 1851:17; Strauch, 1862: 41; 1890:91; Bocourt, 1876,394; Gray, 1873:113; Dugès, 1869:143; 1894:375; 1896:479.

Kinosternum leucostomum LeConte, 1854:183; Müller, 1885:716.

Swanka maculata Gray, 1855:68. Type locality: Vera Paz, Guatemala, and Cosamaloapam, Veracruz (México). Restricted to the latter by Smith and Taylor (1950b:25). Gray, 1869:69.

Swanka leucostoma Gray, 1855:69.

Kinosternon leucostomum Gray, 1855:46; Stuart, 1934:5; 1948:44; Wettstein, 1934:15; Schmidt, 1941:488; 1946:5; Smith and Taylor, 1950b:25; Mertens and Wermuth, 1955:337; Alvarez del Toro, 1960: 45; 1973:20; Wermuth and Mertens, 1961:22; Duellman, 1963:231;

1965:592; Casas Andreu, 1965:381; 1967:49; Legler, 1965:619; Neill, 1965:117; Pritchard, 1967:40; Savage, 1973:9; Iverson, 1976:258.

Thyrosternum leucostomum LeConte, 1859:6; Troschel, 1860:270.

Cinosternum leucostomum Cope, 1865:189; 1885:389; 1887:22; Boulenger, 1889:42; Siebenrock, 1906:97; 1907:581; 1909:446; Barbour and Cole, 1906: 148.

Cinosternum brevigulare Günther, 1885:17; (non Cinosternum brevigulare Cope, 1885:389). Type locality: Playa Vicente, México. Cope, 1887:23.

Cinosternum cobanum Gunther, 1885:17. Type locality: Cobán and Cahabon, Guatemala. Restricted to the former by Smith and Taylor (1950b:25). Cope, 1887:23; Atkinson, 1907:152; Stuart, 1948:44.

Kinosternon mopanum Neill, 1965:117. Type locality: Waha Leaf Creek, southern Stann Creek District, British Honduras (Belize). Iverson, 1976:258.

Kinosternon leucostomun Alvarez del Toro, 1973:165.

Diagnosis

Kinosternon leucostomum is a medium-sized Kinosternon (males reach 174 mm CL, females reach 158 mm CL) which can be distinguished from other Kinosternon by the following combination of characters in adults: (1) carapace of intermediate height and width; (2) carapace generally bearing a single median keel or no keel; lateral keels faint or absent, always less prominent than median keel; (3) C1 usually (88.5% of individuals) contacts M2; (4) M11 usually (73.9%) higher than M10; (5) inguinal and axillary scutes usually (81.9%) not in contact, never in broad contact; (6) plastron large, may or may not completely close ventral openings of shell; (7) posterior plastral lobe more or less evenly rounded, anal notch small or lacking; (8) gular scute less than 60% of anterior plastral lobe length, and wider dorsally than ventrally; (9) abdominal scute short; and (10) adult males with clasping organs on posterior thigh and leg, lacking in females.

Description

Carapace of intermediate width (Table 44), generally ovoid (CWN = ♂♂ 6.42, ♀♀ 6.31). Shell variably depressed (Table 44). Carapace weakly unicarinate or non-carinate, occasional juveniles with faint lateral keels, but central keel always more prominent. C1 usually (88.5%) contacts M2 (M2C = 1.77). M11 usually (74%) higher than M10 (M11 = .521).

Plastron variablein size, may or may not completely close the ventral opening of the shell. Anal notch lacking or very slightly emarginate, more emarginate in males than in females. Interanal seam long, interabdominal seam short, gular scute short (Table 44). Inguinal and axillary scutes in contact in 28.2% of individuals (AIC = .363), never in broad contact. Bridge of intermediate length (Table 44).

Clasping organs (Legler, 1965) present on the posterior thighs and legs of adult males, absent in females.

Color and pattern

Carapace dark straw, brown, or black, or mottled combinations of these. Interlaminal seams dark brown or black. Smaller specimens often with carapacal scutes dark yellow or pale brown at growth center of each scute (posteromedial region on central and pleural scutes, posterolateral region of each marginal), gradually darker away from each growth center.

Plastron and ventral surfaces of marginal scutes yellow to straw or dark brown (scutes carefully cleaned of chemical deposits from the water). Interlaminal seams dark brown to black.

Head with dark gray, brown, or black ground color dorsally and laterally. Two broad yellow, cream, straw, or brown stripes extend from rear margin of orbit to lateral surfaces of neck. In immature and subadult specimens, head stripes are bright yellow or cream in bold contrast to dark gray or brown ground color. In young adults, head colors gradually darken and colors become more obscure; pale yellow or gold flecks frequently appear on postorbital stripes, less frequently scattered on dorsum of head. In older, larger adults, dark brown or black dots partially or completely obscure postorbital stripes.

Head and neck pale gray, cream, straw, or brown ventrally, usually with numerous darker spots, rarely immaculate. Limbs and tail neutral gray or brown above, often with many darker spots; pale gray or cream ventrally.

Jaw sheaths with cream, straw, or light brown ground color, frequently with dark vertical streaks in adult males; immaculate in most juveniles, females, and many males. Iris in living specimens generally orange in females, darker orange in males. In both of the sexes, deposits of melanin around pupil form stellate pattern.

Geographic range

The geographic range of Kinosternon leucostomum is shown in Figs. 7-8. The northern limit of the known range is the series of short rivers just south of the Sierra Volcánica Transversal at Punta del Morro, Veracruz, México. Several other tropical turtles reach the northern limit of their distribution here (e.g., Pseudemys scripta venusta, Claudius angustatus, Staurotypus triporcatus, Kinosternon acutum, and Dermatemys mawi). The geographic range of K. leucostomum includes all Gulf of México drainages from the Río Papaloapan basin to the Río Usamacinta (populations A-C). On the Caribbean Coast, it occupies nearly all drainages from the southeastern Yucatan Peninsula throughout Central America, to the Ríos Atrato and Magdalena on mainland South America (populations D-M, S, and U). K. leucostomum is also known from several localities on the Pacific Coast of Central America associated with the three largest peninsulas (Nicoya, Osa, and Azuero). The species occurs in the Río Chucunaque basin in Panamá, and on mainland South America from the Río San Juan, Colombia to the Río Daule near Guayaquíl, Ecuador.

Specific localities for Kinosternon leucostomum are listed by Barbour and Cole (1906); Boulenger (1889, 1898, 1913); Casas Andreu (1967); Cope (1865, 1875, 1876, 1885); Duellman (1963, 1965); Dugès (1869); Dumeril, Bibron, and Dumeril (1851); Günther (1885-1902); Lee (1977); Medem (1957, 1962); Meyer and Wilson (1959); Moll and Legler (1971); Neill (1965); Neill and Allen (1959); Schmidt (1941, 1946, 1947); Siebenrock (1906, 1907); Smith (1938, 1960a, 1960b), Stuart (1934, 1935, 1943, 1948, 1958); and Villa (1973).

Natural history

K. leucostomum occurs in a variety of aquatic habitats throughout its geographic range. It prefers somewhat more permanent aquatic situations than does *K. scorpioides*, but the geographic range of *K. leucostomum* includes fewer xeric habitats.

Moll and Legler (1971) found *K. leucostomum* "common in most fresh-water habitats within its range [in Panamá]. Adults of both sexes frequently leave the water and wander about on land". Legler (1966) collected *leucostomum* in northern Costa Rica in fast water streams where *K. angustipons* was absent. Medem (1962) collected *leucostomum* in Colombia (as "*spurrelli*") in slow water, in pools and swamps, and in small streams, and said they entered brackish or even salt water near the mouth of the Río San Juan (Pacific) in western Colombia.

Meyer and Wilson (1973) found that the species occurred from sea level to 750 m elevation in Tropical Moist Forest, Tropical Dry Forest, and Subtropical Wet Forest associations in streams and ponds during day or night, or on roads after rains. In El Petén, Guatemala, Duellman (1963) found *leucostomum* on the forest floor and in small sluggish streams. Stuart (1948) stated "it occurs in relative abundance during the rainy season [in Alta Verapáz, Guatemala]. At Finca Chama it was secured in shallow water holes, and at Panzos was common in flooded second growth. During the dry season it was present in a spring at Panzos."

Remarks

The type locality of *Kinosternon leucostomum* has been restricted twice from Dumeril, Bibron, and Dumeril's (1851) "N. Orleans; Mexique;

Río-Sumasinta"; first by Schmidt (1941) to "Río Usamacinta, Peten, Guatemala", and next by Smith and Taylor (1950b) to "Cosamaloapam: Veracruz: Mexico." Both restrictions were without additional comment. As Stuart (1941) has pointed out, Schmidt (1941) simply corrected the misspelling of the Río Usamacinta, and restricted the type locality to a region from which M. Morelet (who obtained the type specimens) was known to have received specimens of other reptiles. Smith and Taylor (1950b) restricted the type locality to "Cosamaloapam: Veracruz: Mexico" apparently because it was the type locality for the next oldest taxon referable to _K_. _leucostomum_, that being _Swanka_ _maculata_ Gray (1855). Interestingly, the type locality of _Swanka_ _maculata_ was restricted to Cosamaloapam in the same paper (_viz_ Smith and Taylor, 1950b). For the reasons stated above, and since it is senior to Smith and Taylor's (1950b) restriction, Schmidt's (1941) restriction is valid and should be recognized as the restricted type locality for _Kinosternon_ _leucostomum_ Dumeril, Bibron, and Dumeril.

Recent reviewers have continued to treat _K_. _leucostomum_, _K_. _postinguinale_, and _K_. _spurrelli_ as distinct species (_cf_. Wermuth and Mertens, 1961; Pritchard, 1967). Nevertheless, Hartweg (in Schmidt, 1946) and Legler (1965) have considered the variation between the taxa to be clinal, and have proposed (or implied) that all are members of a single species.

It is clear that there are only two groups of populations which are consistently phenetically discrete, although the results of the phenetic analyses of _K_. _leucostomum_ are somewhat ambiguous. These are the groups of populations A-G (southern Mexico, south to the Mosquito

Lowlands of Nicaragua), and J-U (the Río San Juan basin on the Nicaragua-Costa Rica border, south to Colombia and Ecuador). The subspecific names which must be applied to these groups are K. leucostomum leucostomum, and K. leucostomum postinguinale, respectively. Populations H-I (southern Mosquito Lowlands and Corn Island) are phenetically and geographically intermediate, and constitute intergrade populations. Variation within these taxa will be discussed below.

Kinosternon leucostomum leucostomum
Dumeril, Bibron, and Dumeril
(Fig. 33)

Cinosternon leucostomum (in part) Dumeril, Bibron, and Dumeril, 1851:17. Type locality: "N. Orleans; Mexique; Río-Sumasinta." Restricted by Schmidt (1941:488) to Río Usamacinta, Petén, Guatemala.

(See species synonymies.)

Diagnosis

Individuals of K. l. leucostomum can be distinguished from members of the other subspecies by the following combination of characters in adults (cf. Table 44): (1) carapace relatively high; (2) plastron extensive (plastral index = ♂♂ .73/.69, ♀♀ .73/.70; (3) gular scute relatively long, interabdominal seam short, interanal seam long (interlaminal seams of plastron at midline: ♂♂ = .15-.14-.04-.21-.07-.29; ♀♀ = .14-.15-.03-.21-.06-.31); (4) inguinal and axillary scutes in contact in 27.2% of individuals examined (AIC = .617); (5) head relatively larger (HW = ♂♂ .20, ♀♀ .19; (6) clasping organs in males poorly developed; and (7) head pattern variable, but postorbital stripes generally more obscure than in K. l. postinguinale (Fig. 33 E-F).

Color and pattern

Color and pattern of carapace and plastron as described under K. leucostomum above. Juvenile pattern as described above. Postorbital stripes in adults generally obscure due to gradual deposition of melanin early in development. In oldest, largest individuals, all trace of postorbital striping often absent.

Geographic range

K. leucostomum leucostomum is known from the Atlantic drainages of México from the Sierra Volcánica Transversal 70 km north of Veracruz to the Río Usamacinta draining most of the Guatemalan Plateau. It occupies Caribbean drainages from the southeastern Yucatan Peninsula more-or-less continuously to the northern portion of the Nicaraguan Mosquito Lowlands (populations A-G).

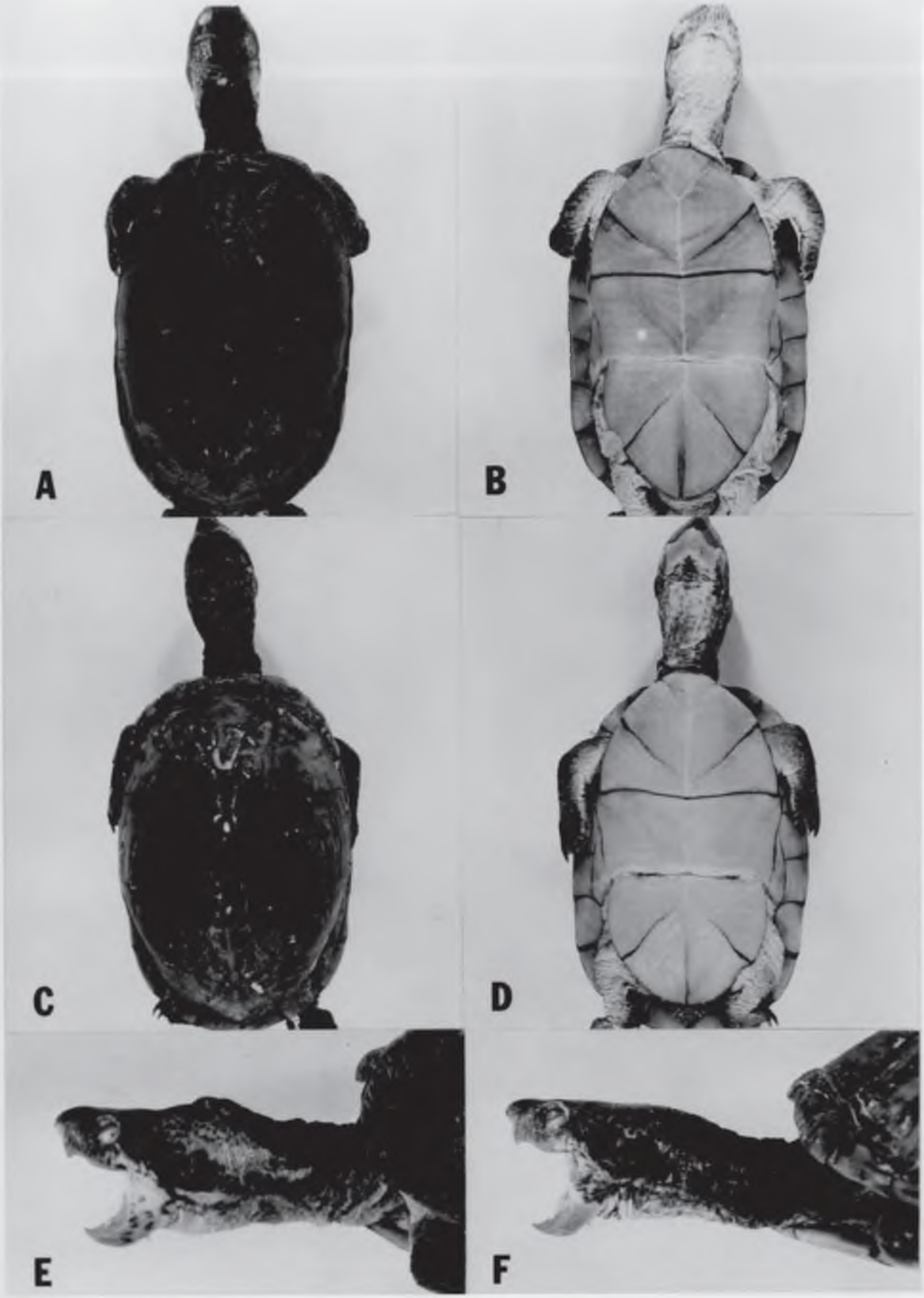
K. l. leucostomum is not known from the eastern, central, or northern portions of the Yucatan Peninsula where it is apparently replaced by K. creaseri. The only other possible hiatus in the range is the north-central coast of Honduras where the northern Sierras are especially close to the coast reducing the coastal lowlands to a narrow strip, but this is also an area from which systematic turtle collections are lacking.

In the southern portion of the Nicaraguan Mosquito Lowlands (populations H-I), *K. l. leucostomum* intergrades with *K. l. postinguinale*.

Remarks

K. l. leucostomum is extremely variable in color and pattern as well as in general body form, and has been known by several names. Neill (1965) described *Kinosternon mopanum* from British Honduras (Belize) which was said to differ from *K. leucostomum* in having: (1) gular scute less than 1/2 anterior lobe length; (2) the axillary and inguinal scutes separate; (3) head color is "a clear, light yellowish-brown with a sharply defined black postorbital stripe and a sharply defined sagittate figure on the crown"; and (4) hands and feet small. Iverson (1976) challenged Neill's description pointing out that *K. mopanum* fell within the range of variation of *K. leucostomum*, and placed *K. mopanum* in synonymy with *K. leucostomum*. Results of the present analysis show that: (1) gular length is .39-.52 of anterior lobe length (average .44); (2) axillary and inguinal scutes are in contact in only 27.2% of the cases examined; (3) head color is generally dark in *K. l. leucostomum*, but specimens from Belize (population D) generally possess more clearly defined and brightly colored head stripes than do those from Veracruz, Mexico (population A) from which Neill (1965) obtained at least part of his comparative material; and (4) in my experience the size of the hands and feet is quite individually and ontogenetically variable, and constitutes such a subjective character that it cannot be used effectively in diagnosing any kinosternid taxon. In conclusion, the results of this study support Iverson's (1976) synonymy completely; *K. mopanum* should be considered

Figure 33. Dorsal, ventral, and head views of Kinosternon leucostomum leucostomum male (A-B, E: UU 9521, CL=124 mm), and female (C-D, F: UU 9526, CL=116 mm, both from Río Tabasquillo nr Frontera, Tabasco, México). Head views X .56.


A
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a subjective junior synonym for K. leucostomum leucostomum.

Günther (1885) described Cinosternum cobanum from Cobán and Cohabon, Guatemala, suggesting it had an immovable posterior plastral lobe. However, Hartweg (in Stuart, 1948) noted that this is a juvenile character which occasionally persists in adults, and that Günther's specimens were juveniles.

Kinosternon leucostomum postinguinale Cope

(Fig. 34)

Cinosternon leucostomum (part) Dumeril, Bibron, and Dumeril, 1851:17. Type locality: "Vallée de La Madeleine (N. Grenada; Santa Fe de Bogotá (N. Grenada)." Dumeril and Dumeril, 1851:17; Bocourt, 1876:394.

Cinosternon leucostomum (part) Cope, 1865:189; 1876:153; Boulenger, 1889:42; 1898:108; Siebenrock, 1907:581.

Cinosternum brevigulare Cope, 1885:389 (not Cinosternum brevigulare Günther, 1885:17). Type locality: "Tierra Calliente of Costa Rica at Sipurio, on the east coast."

Cinosternum postinguinale Cope, 1887:23 (substitute name for Cinosternum brevigulare Cope, 1885:389).

Cinosternum spurrelli Boulenger, 1913:1030. Type locality: Peña Lisa, Condota, Colombia.

Kinosternon postinguinale Schmidt, 1946:4; 1947:109; Mertens and Wermuth, 1955:337; Wermuth and Mertens, 1961:22; Medem, 1962:282; Pritchard, 1967:40.

Kinosternon leucostomum Schmidt, 1946:5; Stuart, 1963:48; Legler, 1965:621; Moll and Legler, 1971:89; Savage, 1973:9.

Kinosternon spurrelli Mertens and Wermuth, 1955:338; Medem, 1957:16; 1961:453; 1962:282; Schmidt, 1946:5; 1947:109.

Kinosternon postinguinal Legler, 1965:621.

Diagnosis

Individuals of *K. leucostomum postinguinale* can be distinguished from members of *K. l. leucostomum* by the following combination of characters in adults (*cf.* Table 44): (1) carapace relatively depressed; (2) plastron relatively smaller (plastral index = ♂♂ .69/.66, ♀♀ .71.68; (3) gular scute relatively short, interabdominal seam long, interanal seam short (interlaminal seams of plastron at midline: ♂♂ = .12-.14-.05-.23-.06-.27; ♀♀ = .12-.15-.04-.23-.06-.29); (4) inguinal and axillary scutes in contact in 12.7% of individuals examined (AIC = .261); (5) head relatively smaller (HW = ♂♂ .19, ♀♀ .18); (6) clasping organs in males well developed; and (7) head pattern variable, but postorbital stripes generally more distinct and brightly colored (i.e., resembling juvenile pattern) than in *K. l. leucostomum* (Fig. 34 E-F).

Color and pattern

Color and pattern of carapace and plastron as described under *K. leucostomum* above. Juvenile pattern as described above. Postorbital stripes in adults generally and brightly colored (Fig. 34 E-F); color of stripe yellow, straw, or pale brown. Developmental pattern is one of retention of juvenile pattern in young adults, but gradual deposition of melanin eventually obscures postorbital stripes in oldest and largest individuals.

Geographic range

K. leucostomum postinguinale is known from Caribbean drainages from the Río San Juan and Lago de Nicaragua on the Nicaragua-Costa Rica border, southward more-or-less continuously to the Ríos Atrato and Magdalena in Colombia (populations J-M, S, U).

While its range is primarily Caribbean, *K. l. postinguinale* is known from several isolated localities on Pacific drainages all associated with large Central American Peninsulas. In northwestern Costa Rica, it occurs in drainages into Golfo de Nicoya and the Nicoya Peninsula (population N). Further to the southeast, specimens are known from the short rivers emptying into Golfo Dulce and Peninsula de Osa (population O). Still further east, a single specimen (FMNH 68114) from near Chitre, Herrera, Panamá suggests *K. l. postinguinale* occurs at the base of the Peninsula de Azuero. It is known from the Río Chucanaque basin, Darien, Panamá (population R), and on the mainland of South America from the Río San Juan basin, Colombia, at least to the Río Daule near Guayaquíl, Ecuador (population T).

Remarks

Since its description by Boulenger (1913), most authors have referred to *Kinosternon spurrelli* as a species distinct from *K. leucostomum* (Dunn, 1945; Mertens and Wermuth, 1955; Medem, 1959, 1961, 1962; Wermuth and Mertens, 1961; Pritchard, 1967). Hartweg (*in* Schmidt, 1946) and Legler (1965) both suggested that *spurrelli* was actually a synonym for *leucostomum*. The phenetic analyses presented here clearly indicates that South American populations (including specimens from population T, which is very near the type locality for spurrelli on the Río San Juan, Colombia) are not phenetically distinct from those in southern Central America. Furthermore, there is no evidence that any of the characters mentioned by Boulenger (1913) or Pritchard (1967) will satisfactorily diagnose South or Central American populations, or that coloration of the head or shell is consistently or significantly different (Wermuth and Mertens, 1961). I conclude that the name spurrelli should be placed in synonymy with K. leucostomum postinguinale.

Dr. A. Rhodin (pers. comm.) has examined large series of leucostomum in the possession of Dr. F. Medem which I have not seen, and he is reasonably convinced that there are distinctive high and low elevation forms present in northwestern Colombia, but the relationship of these to spurrelli and postinguinale remains unknown.

Figure 34. Dorsal, ventral, and head views of *Kinosternon leucostomum postinguinale* male (A-B, E: UU 8842, CL=138 mm), and female (C-D, F: UU 8809, CL=129 mm, both from Juan Mina, Canal Zone). Head views X .56.

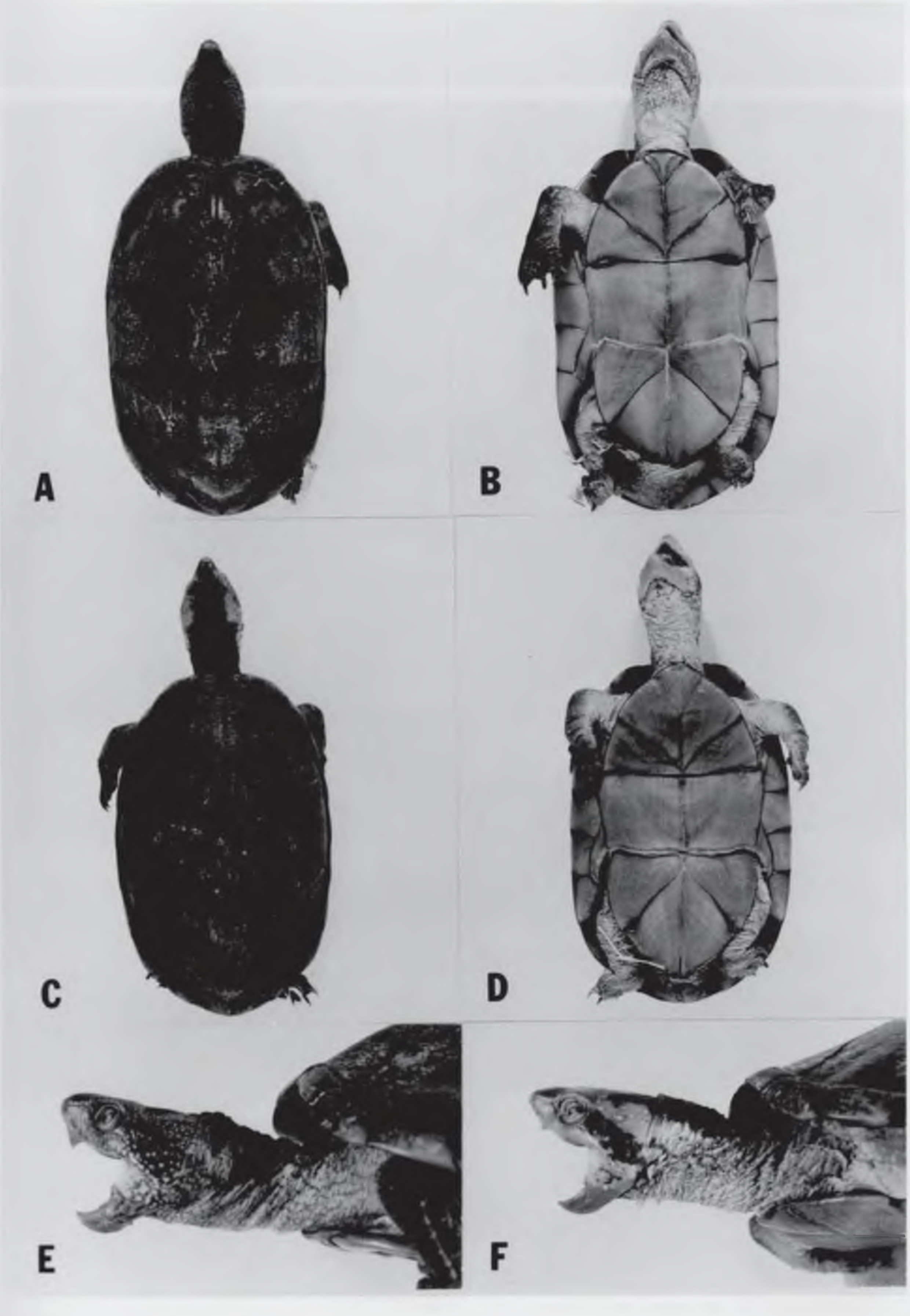
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Table 44. Characters useful in distinguishing the subspecies of Kinosternon leucostomum. Values are expressed as a mean (above) and range (below) of each character as a proportion of CL.

	CWA	CWP	SHT	AHW	TFW	BRL	GUL	ABL	ANL
MALES									
K. l. leucostomum	.62	.62	.39	.45	.43	.24	.15	.21	.29
	.58-.65	.57-.65	.33-.45	.42-.49	.38-.46	.22-.26	.10-.18	.18-.25	.24-.33
K. l. postinguinale	.62	.62	.37	.43	.41	.24	.12	.23	.27
	.57-.70	.55-.70	.31-.39	.37-.51	.35-.46	.20-.28	.08-.16	.20-.27	.22-.24
FEMALES									
K. l. leucostomum	.63	.63	.42	.47	.47	.26	.14	.21	.31
	.59-.68	.59-.68	.36-.50	.41-.52	.41-.49	.22-.30	.11-.18	.19-.24	.24-.36
K. l. postinguinale	.62	.63	.39	.45	.43	.25	.12	.23	.29
	.58-.68	.56-.68	.34-.48	.38-.48	.39-.47	.22-.29	.09-.16	.20-.27	.25-.35

DISTRIBUTIONAL HISTORIES

The distributional histories of the *Kinosternon scorpioides* and *K. leucostomum* complexes (like nearly all vertebrates in the same region) is strictly inferential since no fossil record is known. Nevertheless, a substantial body of distributional information on other vertebrate groups permits the drawing of reasonably reliable inferences. I have attempted to cite only summarizing or review articles in the following discussion. Lengthy discussions of the general biogeographic patterns noted below can be found in these summaries, or in the extensive bibliographies they contain.

Members of the genus *Kinosternon* are not absolutely restricted to aquatic habitats. This makes any explanation of distributional patterns somewhat more difficult than in fishes or thoroughly aquatic kinosternids like *Sternotherus minor* (Iverson, 1977). The geographic ranges of *Kinosternon* populations are likely limited by a combination of geologic and environmental barriers (e.g., deserts, mountain ranges).

Early biogeographers (e.g., Dunn, 1931, 1940) regarded *Kinosternon* as an "Old Northern", or North American derivative which expanded its range southward during Cenozoic time. Savage (1960, 1966) suggested instead that *Kinosternon* (at least the Central American forms) arose within Nuclear Central America. Information presently available on the evolution of the Kinosternidae suggests two different, contradictory origins for the family: (1) D. M. Bramble (pers. comm.) has demonstrated that the kinosternids arose from dermatemydid ancestors during the early Cenozoic (Paleocene to Oligocene) of the northern Great Plains of North America; but (2) the area of greatest diversity of living kinosternids is northern Central America with four species of *Kinosternon*, all members of the genera *Claudius* and *Staurotypus*, plus the only extant dermatemydid, *Dermatemys mawii*, implying the Kinosternidae may have arisen in northern Central America.

The relationships among the members of the *Kinosternon scorpioides* and *K. leucostomum* complexes are generally unknown. Frair (1972) has presented evidence based on blood serum electrophoresis that *K. scorpioides* (as *scorpioides* and *cruentatum*) and *K. leucostomum* form a natural group distinct from North American species. My own work (not necessarily the present study) tends to support Frair's (1972) arrangement; i.e., the *K. scorpioides* and *K. leucostomum* complexes are more closely related to each other (and to other Central American *Kinosternon*) than either is to North American species.

Kinosternon scorpioides Complex

The following proposed evolutionary and distributional histories are considered to be both logical and parsimonious. These proposed histories are based on the results of the analyses presented in this study of phenetic relationships among populations, and information on distributional patterns in Central American and Mexican reptiles, amphibians, and fishes (see reviews in Savage, 1960, 1966; Duellman, 1966, 1970; Miller, 1966; Myers, 1966; and Stuart, 1964, 1966).

I propose that the Kinosternon scorpioides complex arose in the mesic lowlands of southern Mexico or northern Central America during the middle Cenozoic from a primitive and generalized Mexican-Central American stock. During the Miocene, considerable uplifting of mountain ranges in the area combined with gradually increasing aridity at the Isthmus of Tehuantepec partitioned this primitive "scorpioides" stock into a southern Mexican group and a nuclear Central American group (see Stuart, 1966 and Durham et al., 1955 on the proposition that México and Central America have never been separated by a seaway at the Isthmus of Tehuantepec).

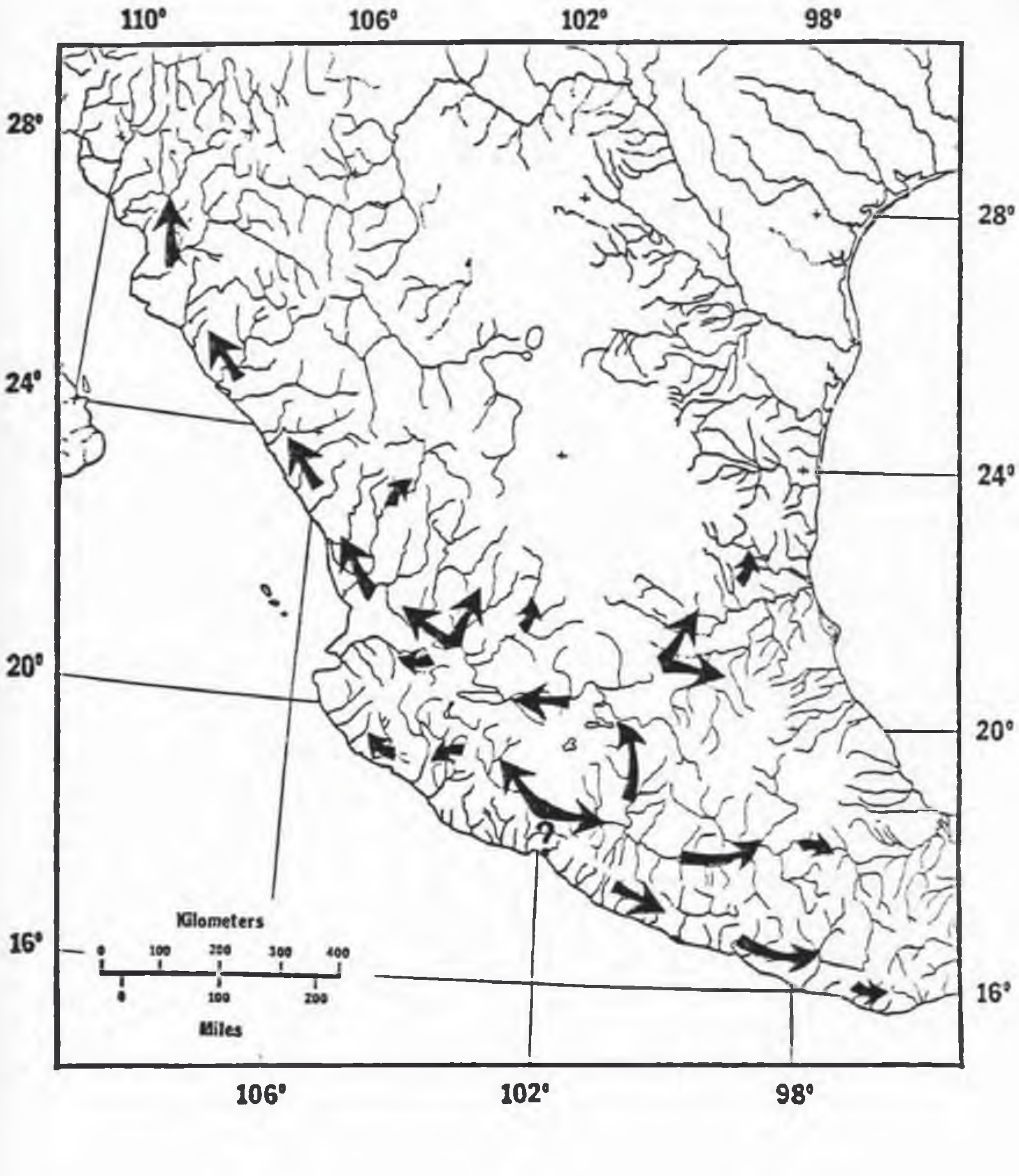
The populations of primitive "scorpioides" thus isolated in southern México occupied the mesic to semi-arid Pacific Coast and gradually differentiated into southern Pacific integrum. As mountain formation and aridity proceeded in southern México, these primitive integrum occupied the Río Balsas basin, and gradually gained access to the Mexican Plateau via the proximity of the northern headwaters of the Balsas system to the developing Lerma system (see Barbour, 1975 for precedent in fish). The phenetic intermediacy of the upper Río Balsas populations between southern Pacific Coast and Plateau populations is evidence of continuing gene flow. The directionality of this dispersal is, unfortunately, questionable. An alternative that I find less attractive is that integrum arose in what is now the Mexican Plateau from a scorpioides-like ancestor and dispersed southward into the Río Balsas basin. Proposed dispersal patterns for

K. integrum are shown in Fig. 35.

Having gained access to the Río Lerma, *K. integrum* spread over most of the Mexican Plateau via the tributaries of the Río Lerma. The northern Pacific Coast was almost certainly colonized directly from the Mexican Plateau populations (based on their extreme phenetic homogeneity) via the Río Grande de Santiago, possibly during a time in late Pliocene or very early Pleistocene preceding the uplift of the Plateau and subsequent change in stream gradient (Maldonado-Koerdell, 1964; Savage, 1960, 1966). Barbour (1975) has suggested that the ancestral Río Grande de Santiago may have utilized the present Ríos Ameca and/or Tuxpan as an outlet to the sea, and the phenetic similarity of the *Kinosternon integrum* populations in the latter drainages to those of the Río Lerma basin would seem to support this contention. However, the possibility that these drainages were colonized by overland migration of *integrum* across the narrow Pacific Coastal Plain, or across the narrow gap between the Laguna de Atotonilco Valley and the upper Río Ameca cannot be ignored.

K. integrum almost certainly gained access to the upper Río Pánuco-Tamesí system by headwater stream erosion and subsequent stream capture of portions of the easternmost Río Lerma by the Río Pánuco (Santa María). The fish fauna of the upper Río Pánuco is more nearly typical of the Río Lerma than that of the lower Río Pánuco (Gregg, (1956). Hubbs and Miller (1977) have suggested a similar stream capture of the southeastern Río Lerma by the encroaching headwaters of the Río Papaloapan based on the presence of the cyprinid minnow "*Hybopsis*" *moralesi* in the latter system. Again, the possibility of

Figure 35. Proposed dispersal routes of *Kinosternon integrum* in México. Explanations of these routes appear in the text.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dispersal by overland migration by _K. integrum_ could account for its presence in both the upper Pánuco-Tamesí and Papaloapan basins.

The phenetic similarity of northern Pacific Coast (Río Ameca northward) _K. integrum_ to those of the Mexican Plateau suggests the former is more likely derived from the latter than from southern Pacific Coast (Ríos Armería southward) populations. The distribution of _K. integrum_ along the northern Pacific Coast is nearly continuous as far north as the lower Río Yaqui in coastal lowland rivers and swamps. Meek (1904) noted that much of the fish fauna of the Río Yaqui and the drainages to the south was derived from the upper Río Grande-Conchos system by stream capture by the Yaqui system. The lack of specimens of _Kinosternon integrum_ from the upper Río Grande or Conchos, or from any of the independent interior basins which were once a part of these rivers (Conant, 1969, _in press_; Morafka, 1977) argues against such an origin for _K. integrum_. Numerous museum records of _integrum_ from interior Chihuahuan Desert drainage localities (e.g., Río Nazas) actually are misidentified specimens of _K. hirtipes_, or _K. integrum_ from localities on the upper Río San Pedro-Mezquital or Río Grande de Santiago based on my examination of pertinent museum specimens.

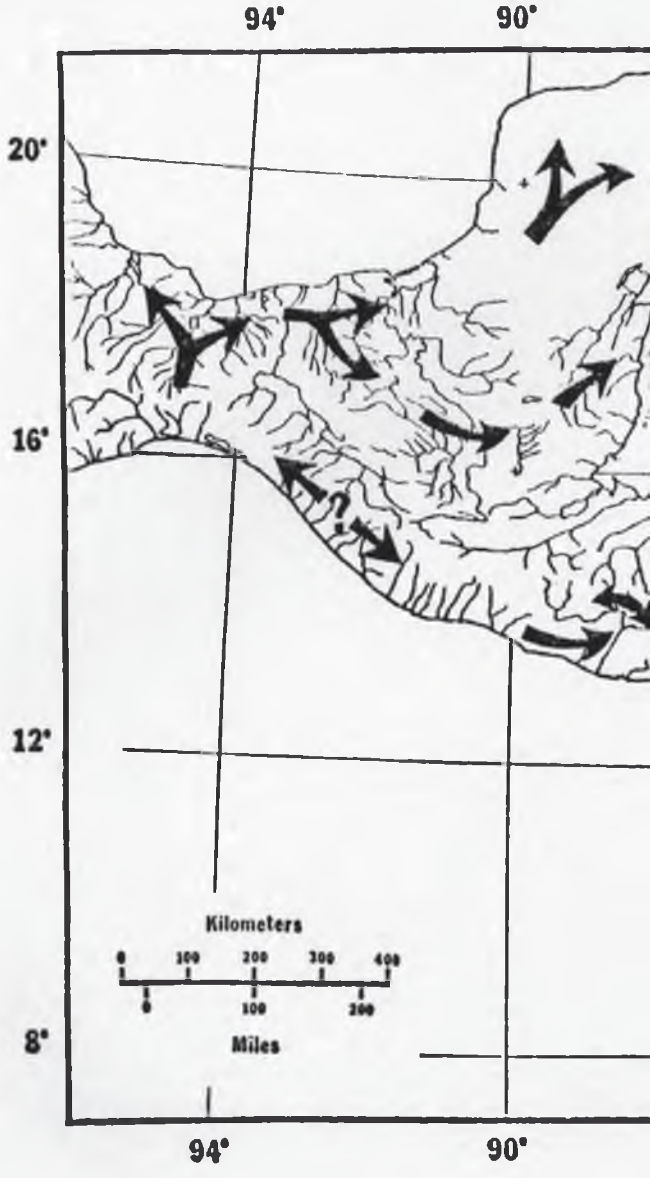
The origin of _Kinosternon alamosae_ is problematical. It may have arisen in southern Sonora (near the type locality) as the result of the isolation of a portion of the range of a primitive _integrum_ stock by the uplifting of the Sierra Madre Occidental. During a lengthy period of isolation, _alamosae_ became adapted to the increasingly xeric conditions on the northern Pacific Coast. Alternatively, _alamosae_ may have arisen to the east of the developing Sierra Madre, and dispersed into southern Sonora via the Río Mayo or Fuerte (a pattern noted in fish by Meek, 1904; and *Pseudemys* turtles by Legler, pers. comm.; Legler and Webb, 1970). I consider the former explanation the more logical and parsimonious.

Following the mid-Cenozoic partitioning of the primitive *scorpioides*-group stock, the nuclear Central American group was subjected to the gradually harshening and increasingly xeric conditions which dominated the region (Maldonado-Koerdell, 1964; Savage, 1966). As the Central American mountain ranges developed, *Kinosternon scorpioides* was forced into relatively xeric refugia along the narrow Pacific Coastal Lowlands. It was probably during this time that the "temporary-water" adapted morphology of *K. scorpioides* arose, with subsequent differentiation (and, ultimately, speciation) from the more generalized *integrum*-like morphology. With the increasing uplift of Central America during the Pliocene, *scorpioides* was able to disperse further southward in Central America, but always along the relatively xeric Pacific Coast; the developing Central American Volcanic Axis and uplifted highlands forming a nearly complete barrier to dispersal between the Pacific and Caribbean Coasts.

Proposed dispersal patterns for *K. scorpioides* are shown in Fig. 36.

K. scorpioides has traversed the Central American highlands in at least one place. The Río Coco and other Caribbean drainages of the Nicaraguan Mosquito Lowlands have probably captured the headwaters of some Pacific Coast streams in southern Honduras and/or northern

Figure 36. Proposed dispersal routes of _Kinosternon scorpioides_ in Central America. Explanations of these routes appear in the text.



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86°
82°
78°

Nicaragua (Stuart, 1966). The consistent phenetic similarity of Caribbean Mosquito Lowlands populations of _K. scorpioides_ to those of the Pacific Coast of Nicaragua seems to suggest this pattern is likely true, although the possibility of terrestrial dispersal across the relatively low Nicaraguan Depression (West, 1964) cannot be discounted. There is general agreement that the Río San Juan which presently drains Lagos de Nicaragua and Managua into the Caribbean captured the formerly Pacific drainages of the lakes and their connection via the Río Tipitapa (_cf_. Stuart, 1966). It is possible that _K. scorpioides_ gained access to the Caribbean Lowlands by dispersal through the Río San Juan, but no specimens of _scorpioides_ have been collected along the river's lower portion in spite of adequate collecting which has yielded many specimens of _Kinosternon leucostomum_, and I favor the former hypothesis.

The population of _K. scorpioides_ on San Andres Island, Colombia (Caribbean) is phenetically most similar to populations on the Caribbean Coast from which it is almost certainly derived. The island lies well east of the continental shelf (Stuart, 1966) suggesting the colonization by _scorpioides_ was via rafting or some similar dispersal mechanism rather than by a land bridge connection with the mainland. The possibility exists that _K. scorpioides_ was introduced onto the islands by humans, since J. M. Legler (pers. comm.) has observed Indians carrying turtles for food or trade in canoes off the coast of Central America.

Primitive _scorpioides_ first entered South America by the Panamanian Isthmian link, probably soon after it was formed.

Estimates of the precise period during which the link was formed vary widely from late Paleocene to mid-Pliocene (cf. Lloyd, 1963; Stuart, 1964, 1966; Savage, 1966, 1973a; Myers, 1966; Raven and Axelrod, 1975; Kiest et al., 1972) with the most recent objective estimate (Emiliani, Gaertner and Lidz, 1972) at 5.7 million years before present (mid-Pliocene). Based on the many similarities between K. integrum (Mexico) and K. s. scorpioides (South America), similarities which were superficially striking enough to cause Siebenrock (1907) to place them in the same subspecies, it seems possible that scorpioides entered South America in early Pliocene prior to the evolution of the xeric-adapted morphology presently seen in intervening Central American populations, possibly by "island hopping" across the intervening isthmus (Raven and Axelrod, 1975). Populations of K. scorpioides from the Peninsula de Azuero and the present Isthmus of Panama are phenetically most similar to northern South American populations (a common pattern in many reptiles and amphibians; see Savage, 1966), and undergo the familiar "shift" from Pacific Central America to Atlantic South America first noted by Dunn (1940; but see Savage, 1966 and Duellman, 1970).

Following its entry into northern South America, K. scorpioides dispersed throughout northern South America and the Amazon basin. It is likely that scorpioides reached the Río Paraná system of southern South America via the lowlands connecting the two basins in eastern Bolivia and southern Brazil.

In northern Central America, Kinosternon scorpioides was restricted to the narrow Pacific Coast, but was able to cross the

Isthmus of Tehuantepec, thus gaining access to the relatively more mesic Gulf Coast. The timing of the dispersal probably corresponded to the closing of the Tehuantepec Portal during the Pliocene if one existed (Stuart, 1966; Savage, 1966). *K. scorpioides* populations then dispersed widely (and probably quickly) throughout the Gulf Coastal Lowlands of eastern México as far north as the Río Soto la Marina. *K. scorpioides* dispersed northward beyond the xeric region near Punta del Morro in eastern Veracruz, Mexico (the eastward extension of the Sierra Volcanica Transversal) which has acted as a barrier to both north and south dispersal of many aquatic and semiaquatic vertebrates including turtles (*Kinosternon leucostomum*, *K. acutum*, *Staurotypus triporcatus*, *Claudius angustatus*, and *Dermatemys mawei* occur no farther north, while *Kinosternon herrerai* occurs no farther south; see Savage, 1966 for further examples). The fact that *scorpioides* has crossed this barrier where other species have failed is probably an indication of the greater tolerance for dry habitats afforded by the morphology of *scorpioides*.

Similarly, *K. scorpioides* dispersed eastward and northward throughout most of the Yucatán Peninsula, portions of the Guatemalan Highlands, and, ultimately, northern Belize (the last is likely derived directly from Guatemalan Highland populations based on phenetic similarities). That the populations of *scorpioides* (*K. s. cruentatum*) in Gulf Coastal México have their affinities with populations on the Pacific Soconusco Coast of Central America rather than via northward dispersal from the Caribbean Mosquito Lowlands populations (*K. s. albogulare*) is strongly supported by the phenetic similarities of the two former groups.

The most difficult population of scorpioides to explain in terms of dispersal history is K. s. abaxillare which is restricted to the Río Grande de Chiapas (Grijalva) occupying the Chiapas Central Depression of southern México and southeastern Guatemala. As demonstrated earlier, abaxillare has its greatest affinities with K. s. cruentatum X albogulare intergrade populations in the Río Lempa basin of Pacific Coastal El Salvador and Honduras. Stuart (1954) hypothesized a river valley "subhumid corridor" by which xeric adapted terrestrial vertebrates could traverse the region between the Río Grande de Chiapas and the Río Motagua (and Ulúa). Presumably, semi-aquatic Kinosternon scorpioides could follow the same route given periods of unusually heavy rainfall. Stuart (1966) later noted an area "of possible faunal interchange, though not necessarily through stream capture, between tirbutaries of the Río Motagua and headwaters of the Río Lempa", a hypothesis attributed to R. R. Miller. If such a dispersal corridor existed, it could explain the unusual distribution of K. s. abaxillare. However, K. scorpioides is not presently known from the intermediate basin of the Río Motagua as would be expected if it were on the path of dispersal. In order for Stuart's dispersal pattern to be valid for K. scorpioides, it is necessary to invoke an argument of local extirpation of K. scorpioides populations in the upper Río Motagua, which seems unlikely to me. The distributional history of Chiapas Central Depression scorpioides remains problematical.

Kinosternon leucostomum Complex

The distributional history of Kinosternon leucostomum is less complex than that of K. scorpioides, chiefly due to its intolerance of xeric environments and its subsequent restriction to mesic lowlands along Caribbean Central America. Proposed dispersal patterns are shown in Fig. 37.

I propose that K. leucostomum, like K. scorpioides, arose in the region of southern Mexico and northern Central America during mid-Cenozoic. As noted above, my own observations are in general agreement with Frair's (1972) biochemical evidence suggesting the K. leucostomum and K. scorpioides complexes form a natural group more closely related to each other than either is to North American Kinosternon.

K. leucostomum was apparently restricted to the relatively mesic lowlands north and east of the Sierra during the period of volcanic activity in late Miocene (a period of rapid uplift of Central American highlands, and generally worsening aquatic conditions in Pacific Central America and the Isthmus of Tehuantepec). As Central America gradually rose during the late Miocene and Pliocene, leucostomum gradually dispersed southward, but always in the relatively mesic Caribbean Lowlands. Once a Panamanian Isthmian link with South America was complete (presumably at mid-Pliocene, but see above) leucostomum dispersed into northwestern South America. In accordance with the familiar crossover pattern noted by Dunn (1940), leucostomum, with its primarily Caribbean distribution in Central America, is widely distributed in the Pacific Chocoan Lowlands of coastal

Figure 37. Proposed dispersal routes of Kinosternon leucostomum in Central America. Explanations of these routes appear in the text.


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Kilometers
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0 100 200
Miles

Colombia, Ecuador and Peru. The situation is somewhat more complicated since _leucostomum_ also occurs in the Caribbean Río Magdalena basin into which it probably dispersed from the Río Atrato by coastal lowland migration, or stream capture of the headwaters of the Atrato by the Magdalena.

While the distribution of _K. leucostomum_ is basically Atlantic, it occurs in Pacific drainages in a few places. _K. leucostomum_ occurs in Pacific drainages into the Golfo de Nicoya in western Costa Rica, and along the shores of Lago de Nicaragua, an area into which it doubtless dispersed via the capture of the large Nicaraguan lakes by the Caribbean Río San Juan (Stuart, 1966). Dispersal may have been aided by the presence of the low Nicaraguan Depression. _K. leucostomum_ also occurs on the relatively mesic Pacific Peninsula de Osa (Golfo Dulce) of western Costa Rica, access to which was likely gained by dispersal across the mesic Caribbean-Pacific corridor across the Talamancan Highlands south of Volcán de Chiriquí discussed by Savage (1966). From the Darien region of Panamá, _leucostomum_ occurs throughout the lowlands of northwestern Pacific South America. Hildebrand (1938) suggested faunal interchange was probable between the Río Tuira (Pacific) of the Darien region, Panamá, and the Río Atrato (Atlantic) of northwestern Colombia, which could account for the phenetic similarities of these populations.

Comparisons of the distributional patterns of _Kinosternon scorpioides_ and _K. leucostomum_ reveals several interesting patterns. As noted previously, the distribution of _scorpioides_ is generally Pacific, while that of _leucostomum_ is generally Atlantic.

Nevertheless, the two species are macro-sympatric in Gulf of Mexico drainages south of Punta del Morro, Veracruz, to the southern portion of the Yucatan Peninsula; in some of the Guatemalan Highlands and northern Belize; in the Caribbean Mosquito Lowlands of Honduras and Nicaragua; and Pacific drainages near the Peninsulas de Nicoya and Osa (and possibly the Peninsula de Azuero).

A relatively greater tolerance for xeric habitats has allowed *K. scorpioides* to invade the Atlantic range of *K. leucostomum* more frequently than the reverse. For example, *scorpioides* has dispersed across the dry Isthmus of Tehuantepec to Gulf of Mexico drainages, while *leucostomum* has not invaded Pacific drainages across the Isthmus. Also, *scorpioides* has dispersed across the relatively dry northern portion of the Yucatan Peninsula while *leucostomum* has not. *K. scorpioides* has crossed the xeric barrier of the Punta del Morro area in coastal Veracruz, Mexico and expanded its range northward, while the range of *leucostomum* extends no farther north. On the other hand, *leucostomum* has dispersed across the mesic Caribbean-Pacific corridor near Golfo Dulce (Savage, 1966) while *scorpioides* has apparently not invaded the Caribbean Coast at this point.

In general, the Atlantic *vs*. Pacific distributional patterns of *leucostomum vs. scorpioides* can be explained as the patterns one would predict given a relatively xeric-adapted Pacific Coast form, and a mesic-adapted Atlantic Coast form.

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APPENDIX 1

Results of Statistical Analyses

(Tables 3-38)

Table 3. Within populations correlation coefficients for Kinosternon leucostomum males, regression standardized (* = significant at .05 level, ** = significant at .01 level).

Character	CWA	CWP	ABL	AHW	PHW	TFW	GUL	HUL	PEL	FEL	ANL
CWA	1.000										
CWP	.695**	1.000									
ABL	.061	.134	1.000								
AHW	.458*	.341	-.034	1.000							
PHW	.523*	.593**	.094	.512 *	1.000						
TFW	.450*	.523*	.114	.569 **	.694**	1.000					
GUL	.023	-.105	-.011	.052	-.016	.011	1.000				
HUL	.117	.159	-.062	.274	.276	.287	-.449	1.000			
PEL	.029	.080	-.037	-.078	-.004	-.021	-.253	-.404	1.000		
FEL	-.030	.038	.018	-.003	-.029	-.048	-.035	-.018	.057	1.000	
ANL	.136	.033	-.072	.353	.244	.296	.120	.196	-.134	-.409	1.000
SHT	.285	.347	.034	.219	.362	.350	-.025	.144	.046	-.052	.200
BRL	.130	.088	.317	.185	.070	.157	.002	-.002	-.029	.022	.079
HW	.230	.140	-.197	.008	.038	.025	.143	-.149	.052	-.029	.020
C1L	.141	.211	.059	.178	.261	.203	-.196	.233	.092	.072	.109
C1A	.186	.182	.038	.155	.213	.128	-.012	.096	.035	.034	.056
C1P	.189	.195	-.030	.082	.179	.104	.079	.075	.002	.031	.078
C3L	.023	.045	.019	.033	.107	.108	.001	.027	-.017	-.045	.041
C3W	.371	.362	.011	.151	.342	.222	-.025	.104	.056	.004	.085
C5L	.003	-.113	-.104	-.053	-.107	-.075	.076	-.112	-.022	.009	-.044
C5W	.038	.073	-.036	-.001	.046	.021	.017	-.062	.043	-.015	-.057
AXL	.205	.197	-.015	.100	.159	.135	-.025	.010	.028	.037	-.045
INL	.164	.226	.170	.075	.198	.197	-.055	.044	.037	.010	-.009
HPW	.278	.145	-.000	.553**	.252	.361	.355	.061	-.147	-.026	.201
FAW	.263	.293	.104	.151	.331	.442*	-.004	.099	.045	-.091	.129
GUW	.051	.040	.034	.127	.061	.100	.335	-.044	-.024	-.001	.020
CWN	.172	-.273	-.007	.146	-.069	-.039	.106	-.007	-.004	-.047	.141
SIM	-.043	-.011	-.036	.001	-.029	-.009	.024	-.016	.015	-.011	-.020
AIC	-.002	-.043	-.064	.052	-.019	-.028	.032	-.014	-.020	.050	.074
M2C	-.005	.015	-.014	-.076	.000	-.000	-.001	-.030	.023	.024	-.061
M11	.136	.119	.054	.135	.178	.126	.017	.094	-.007	-.031	.153

Table 3 (continued)

Character	SHT	BRL	HW	C1L	C1A
SHT	1.000				
BRL	-.005	1.000			
HW	.237	-.049	1.000		
C1L	.238	-.001	-.104	1.000	
C1A	.205	.054	.016	.254	1.000
C1P	.125	-.077	.108	.189	.222
C3L	.214	.080	-.000	.018	.137
C3W	.329	.039	.158	.067	.266
C5L	.005	.006	.233	-.178	-.146
C5W	.006	.019	.019	-.167	-.065
AXL	.177	.013	.094	-.020	.087
INL	.105	.070	-.069	.073	.013
HPW	.152	.107	.054	.056	.103
FAW	.203	.119	.101	.016	.141
GUW	.037	-.044	.012	.077	.174
CWN	-.037	.071	.019	-.043	.053
SIM	-.020	-.014	-.055	.028	.001
AIC	-.025	.055	.112	-.022	.037
M2C	-.023	-.076	.051	.014	-.327
M11	.065	.012	-.010	.154	.017

	INL	HPW	FAW	GUW	CWN
INL	1.000				
HPW	.008	1.000			
FAW	.108	.079	1.000		
GUW	.045	.311	.031	1.000	
CWN	-.074	.158	-.071	.022	1.000
SIM	-.003	.033	.035	.033	-.050
AIC	-.352	.023	-.017	-.069	.034
M2C	-.002	-.021	-.031	.029	-.040
M11	.052	.108	.041	.061	.021

C1P	C3L	C3W	C5L	C5W	AXL
1.000					
.002	1.000				
.186	.171	1.000			
-.087	-.095	.027	1.000		
-.072	-.063	.074	.327	1.000	
.056	.083	.122	.088	.071	1.000
.018	.087	.126	.032	-.031	.385
.115	.000	.037	.018	.011	.027
.058	.053	.237	.048	.138	.090
.134	-.001	.012	-.062	-.026	.019
-.026	.019	.010	.040	-.072	-.058
.021	.041	-.009	-.081	-.016	.006
.055	-.019	-.030	.001	.006	-.338
-.071	.011	-.077	-.075	-.081	-.017
.171	.066	.023	-.216	-.342	-.057

SIM	AIC	M2C	M11
1.000			
-.041	1.000		
.024	-.011	1.000	
.067	.094	.044	1.000

Table 4. Within populations correlation coefficients for Kinosternon leucostomum females, regression standardized (* = significant at .05 level, ** = significant at .01 level).

Character	CWA	CWP	ABL	AHW	PHW	TFW	GUL	HUL	PEL	FEL	ANL
CWA	1.000										
CWP	.712 **	1.000									
ABL	.126	.197	1.000								
AHW	.533 *	.390	.056	1.000							
PHW	.572 **	.614 **	.095	.557**	1.000						
TFW	.410	.499 *	.169	.505*	.671**	1.000					
GUL	-.011	-.104	-.097	.089	-.019	.023	1.000				
HUL	.042	.092	-.075	.204	.202	.147	-.267	1.000			
PEL	.086	.142	.070	-.008	.077	.047	-.223	-.391	1.000		
FEL	-.027	-.092	-.064	-.045	-.096	-.168	.049	-.030	.057	1.000	
ANL	.096	.090	.057	.283	.220	.381	.092	.091	-.049	-.631 **	1.000
SHT	.212	.193	.202	.220	.300	.342	.071	.093	.033	-.177	.366
BRL	.167	.116	.424	.123	.065	.170	.002	-.063	.009	.022	.115
HW	.436 *	.388	-.001	.316	.358	.277	.026	-.019	.102	-.048	.186
C1L	.166	.140	-.151	.117	.168	-.018	-.014	.128	.075	.088	-.074
C1A	.183	.151	-.067	.121	.188	.022	-.038	.159	-.013	.019	-.047
C1P	.138	.138	-.145	.084	.159	-.027	.003	-.006	.016	-.000	-.015
C3L	.068	.043	.136	.094	.152	.207	.041	.078	-.038	-.011	.129
C3W	.364	.385	.003	.216	.405	.234	-.071	.089	.160	-.124	.120
C5L	.001	.006	.003	-.037	-.047	-.014	.036	-.097	.055	-.051	.031
C5W	.064	.154	.078	.013	.059	.130	-.007	-.026	.110	-.050	.004
AXL	.149	.149	.054	.054	.108	.150	.070	.014	.022	.037	.014
INL	.193	.256	.230	.104	.159	.217	-.030	.081	-.028	-.093	.079
HPW	.365	.174	.019	.595 **	.312	.341	.302	.030	-.135	.044	.120
FAW	.285	.343	.264	.130	.347	.385	-.037	.055	.096	-.237	.251
GUW	.137	.124	-.060	.089	.132	-.052	.174	-.041	-.025	.140	-.172
CWN	.105	-.191	-.055	.138	-.074	-.095	.129	-.006	-.055	.097	-.018
SIM	-.022	-.039	-.068	.038	-.037	.009	.035	-.013	-.024	.014	.032
AIC	-.077	-.034	-.093	-.005	-.073	-.075	-.019	.043	-.010	.014	.038
M2C	-.007	-.061	-.056	-.054	-.025	-.032	.037	-.067	.022	.035	-.056
M11	.013	.031	-.082	.016	.056	.003	.020	.062	-.031	.029	.016

Table 4 (continued)

Character	SHT	BRL	HW	C1L	C1A
SHT	1.000				
BRL	.192	1.000			
HW	.311	-.026	1.000		
C1L	-.049	-.158	.075	1.000	
C1A	.014	-.110	.057	.324	1.000
C1P	-.003	-.214	.186	.281	.335
C3L	.295	.124	.084	-.001	.037
C3W	.217	-.087	.219	.095	.270
C5L	.041	.010	.047	-.191	-.214
C5W	.034	.059	.026	-.203	-.090
AXL	.002	-.001	.086	.000	-.017
INL	.176	.176	.010	-.071	-.039
HPW	.156	.030	.255	.135	.051
FAW	.243	.092	.249	-.092	.119
GUW	-.073	-.112	.136	.215	.070
CWN	.007	.090	.010	.043	-.048
SIM	.023	-.039	.026	.120	.000
AIC	-.059	-.013	.054	-.022	.005
M2C	.016	-.096	-.002	.048	-.375
M11	-.039	-.088	.024	.073	.007

	INL	HPW	FAW	GUW	CWN
INL	1.000				
HPW	.097	1.000			
FAW	.132	.035	1.000		
GUW	.070	.246	-.078	1.000	
CWN	.020	.191	-.143	.043	1.000
SIM	-.064	.085	-.048	.022	.074
AIC	-.301	-.097	-.054	-.040	-.008
M2C	-.048	.056	-.053	.090	.016
M11	.017	.080	-.010	.128	-.006

C1P	C3L	C3W	C5L	C5W	AXL
1.000					
.027	1.000				
.181	.165	1.000			
-.009	-.151	-.024	1.000		
-.093	-.128	.128	.499 **	1.000	
-.027	-.036	.076	.081	.107	1.000
-.064	.078	.141	.074	.134	.432 *
.103	.099	.038	-.023	-.112	.110
.019	.145	.289	.080	.155	.094
.111	.008	.070	-.029	-.046	.067
.005	-.066	-.003	.000	-.030	.026
.026	-.044	-.057	.018	-.041	.050
.079	.011	-.041	.011	-.011	-.348
-.103	.003	-.097	.031	.013	-.005
.093	.187	.115	-.053	-.350	.033

SIM	AIC	M2C	M11
1.000			
.066	1.000		
.059	-.005	1.000	
-.006	.070	.029	1.000

Table 5. Within populations correlation coefficients for Kinosternon leucostomum males, ratio standardized (* = significant at .05 level, ** = significant at .01 level).

Character	CWN	CWA	CWP	ABL	AHW	PHW	TFW	GUL	HUL	PEL	FEL
CWN	1.000										
CWA	-.174	1.000									
CWP	.265	.705 **	1.000								
ABL	-.004	.069	.146	1.000							
AHW	-.139	.457 *	.353	-.030	1.000						
PHW	.070	.521 *	.599**	.093	.510*	1.000					
TFW	.041	.450 *	.532*	.115	.561**	.696 **	1.000				
GUL	-.098	.010	-.109	-.005	.046	-.018	.008	1.000			
HUL	.010	.126	.169	-.037	.271	.275	.287	-.454*	1.000		
PEL	-.003	.020	.062	-.040	-.088	-.025	-.043	-.258	-.418	1.000	
FEL	.044	-.019	.038	.016	-.010	-.041	-.060	-.044	-.021	.064	1.000
ANL	-.137	.125	.039	-.051	.349	.239	.302	.111	.186	-.143	-.412
SHT	.039	.288	.349	.020	.222	.368	.352	-.003	.143	.029	-.051
BRL	-.076	.134	.084	.310	.184	.043	.151	-.000	.003	-.029	.000
HW	-.020	.211	.125	-.212	.027	.043	.048	.151	-.128	.038	-.024
C1L	.035	.154	.226	.070	.176	.267	.204	-.180	.225	.076	.082
C1A	-.056	.199	.185	.036	.151	.213	.117	-.015	.093	.032	.029
C1P	.019	.192	.188	-.019	.079	.175	.094	.080	.061	-.009	.045
C3L	-.018	.028	.045	.011	.030	.101	.107	.004	.022	-.020	-.051
C3W	-.015	.379	.366	.002	.161	.342	.223	-.029	.112	.045	-.000
C5L	-.036	-.023	-.141	-.121	-.074	-.142	-.090	.082	-.121	-.013	-.004
C5W	.075	.028	.061	-.060	-.001	.036	.017	.020	-.068	.046	-.028
SIM	-.050	.045	.015	.027	.000	.028	.015	-.030	.018	-.020	.011
AXL	.059	.218	.208	-.012	.102	.173	.135	-.009	.009	.023	.033
INL	.078	.167	.235	.169	.073	.197	.194	-.057	.046	.037	-.006
HPW	-.152	.282	.151	.001	.544	.249	.342	.351	.058	-.157	-.026
FAW	.070	.265	.299	.096	.138	.330	.442 *	-.000	.097	.049	-.096
GUW	-.013	.056	.051	.029	.133	.075	.096	.316	-.030	-.029	.003
AIC	.034	.006	.044	.060	-.064	.012	.017	-.030	.011	.022	-.056
M2C	-.040	-.000	-.011	.020	.071	-.004	-.001	-.006	.023	-.011	-.024
M11	.021	-.139	-.123	-.067	-.128	-.178	-.129	-.006	-.094	.015	.031

Table 5 (continued)

Character	ANL	SHT	BRL	HW	C1L
ANL	1.000				
SHT	.215	1.000			
BRL	.072	-.015	1.000		
HW	.043	.251	-.047	1.000	
C1L	.094	.224	-.006	-.092	1.000
C1A	.055	.199	.041	.020	.244
C1P	.063	.115	-.096	.112	.199
C3L	.042	.191	.075	.027	-.005
C3W	.091	.325	.041	.161	.076
C5L	-.040	.004	.008	.230	-.215
C5W	-.043	.013	.030	.038	-.211
SIM	.021	.018	.017	.058	-.034
AXL	-.041	.161	.015	.099	-.017
INL	.002	.106	.074	-.062	.084
HPW	.190	.158	.112	.068	.058
FAW	.134	.191	.118	.111	.007
GUW	.024	.056	-.050	.016	.112
AIC	-.073	.015	-.054	-.107	.021
M2C	.058	.018	.081	-.050	-.018
M11	-.144	-.064	-.001	.016	-.163

	SIM	AXL	INL	HPW	FAW
SIM	1.000				
AXL	-.004	1.000			
INL	.001	.382	1.000		
HPW	-.034	.037	.004	1.000	
FAW	-.037	.101	.118	.066	1.000
GUW	-.044	.021	.039	.311	.027
AIC	-.041	.340	.352	-.034	.016
M2C	.024	.012	-.003	.012	.022
M11	.067	.051	-.060	-.103	-.041

C1A	C1P	C3L	C3W	C5L	C5W
1.000					
.216	1.000				
.137	-.000	1.000			
.258	.183	.167	1.000		
-.164	-.095	-.094	.014	1.000	
-.076	-.086	-.068	.079	.341	1.000
.003	-.029	-.038	.009	.086	.021
.086	.057	.068	.118	.084	.071
.006	.011	.077	.126	.018	-.034
.103	.106	.007	.045	.005	.001
.122	.047	.055	.230	.049	.131
.183	.149	-.002	.023	-.083	-.060
-.046	-.050	.012	.027	-.001	-.008
.326	.066	-.011	.071	.071	.082
-.020	-.166	-.062	-.016	.214	.334

GUW	AIC	M2C	M11
1.000			
.061	1.000		
-.035	-.011	1.000	
-.065	.094	.044	1.000

Table 6. Within populations correlation coefficients for Kinosternon leucostomum females, ratio standardized (* = significant at.05 level, ** = significant at .01 level).

Character	CWN	CWA	CWP	ABL	AHW	PHW	TFW	GUL	HUL	PEL	FEL
CWN	1.000										
CWA	-.118	1.000									
CWP	.188	.714 **	1.000								
ABL	.049	.132	.183	1.000							
AHW	-.156	.524 *	.380	.088	1.000						
PHW	.063	.572 **	.618 **	.110	.546*	1.000					
TFW	.082	.414	.489*	.206	.509*	.671**	1.000				
GUL	-.129	-.026	-.111	-.042	.091	-.029	.043	1.000			
HUL	.004	.042	.089	-.076	.190	.193	.140	-.272	1.000		
PEL	.054	.098	.142	.068	-.019	.068	.023	-.229	-.410	1.000	
FEL	-.087	-.025	-.082	-.054	-.042	-.090	-.174	.036	-.032	.051	1.000
ANL	.003	.080	.062	.103	.264	.190	.393	.129	.065	-.062	-.632 **
SHT	-.031	.197	.164	.218	.224	.278	.344	.103	.076	.016	-.168
BRL	-.096	.157	.090	.426	.142	.071	.207	.040	-.056	.003	.020
HW	-.022	.427	.377	.025	.325	.344	.268	.012	-.015	.094	-.057
C1L	-.042	.187	.171	-.136	.118	.184	-.021	-.038	.119	.067	.088
C1A	.042	.182	.156	-.051	.138	.186	.021	-.051	.166	-.026	.029
C1P	-.011	.133	.139	-.172	.099	.166	-.032	-.013	-.001	.012	-.003
C3L	.051	.054	.020	.149	.107	.135	.209	.070	.068	-.055	-.012
C3W	-.000	.370	.389	.009	.213	.393	.224	-.080	.080	.161	-.121
C5L	.000	.001	.000	.003	-.038	-.057	-.026	.037	-.100	.053	-.054
C5W	.032	.072	.149	.069	.016	.063	.129	-.003	-.023	.098	-.039
SIM	.074	.018	.031	.056	-.041	.031	-.012	-.024	.014	.019	-.003
AXL	-.032	.150	.141	.068	.047	.109	.139	.073	.005	.026	.029
INL	-.031	.180	.233	.233	.098	.154	.217	-.013	.070	-.019	-.099
HPW	-.199	.352	.167	.059	.594 **	.302	.349	.298	.026	-.144	.043
FAW	.138	.272	.329	.258	.132	.331	.388	-.020	.044	.102	-.238
GUW	-.035	.139	.141	-.045	.083	.130	-.064	.135	-.047	-.011	.118
AIC	-.008	.076	.032	.092	.002	.073	.072	.021	-.049	.021	-.007
M2C	.016	.000	.053	.053	.071	.024	.045	-.024	.074	-.028	-.035
M11	-.006	-.003	-.028	.071	-.006	-.047	.004	-.008	-.057	.036	-.021

Table 6 (continued)

Character	ANL	SHT	BRL	HW	C1L
ANL	1.000				
SHT	.391	1.000			
BRL	.171	.225	1.000		
HW	.176	.307	-.019	1.000	
C1L	-.107	-.069	-.167	.075	1.000
C1A	-.064	.001	-.123	.057	.331
C1P	-.051	-.025	-.242	.185	.314
C3L	.156	.279	.151	.069	-.007
C3W	.095	.189	-.089	.212	.104
C5L	.044	.051	.026	.041	-.183
C5W	.010	.037	.074	.034	-.194
SIM	-.031	-.019	.032	-.027	-.124
AXL	.031	.015	-.008	.088	.004
INL	.104	.191	.180	-.000	-.072
HPW	.119	.162	.043	.244	.134
FAW	.261	.233	.102	.246	-.098
GUW	-.194	-.087	-.127	.121	.229
AIC	-.038	.055	.001	-.058	.028
M2C	.066	-.018	.098	.006	-.045
M11	-.003	.041	.093	-.012	-.063

	SIM	AXL	INL	HPW	FAW
SIM	1.000				
AXL	-.047	1.000			
INL	.062	.434	1.000		
HPW	-.086	.111	.091	1.000	
FAW	.044	.107	.134	.035	1.000
GUW	-.016	.078	.071	.242	-.081
AIC	.066	.355	.301	.097	.053
M2C	.059	-.002	.038	-.044	.051
M11	-.006	-.037	-.021	-.074	.014

C1A	C1P	C3L	C3W	C5L	C5W
1.000					
.346	1.000				
.031	.020	1.000			
.271	.179	.153	1.000		
-.217	-.025	-.143	-.037	1.000	
-.093	-.098	-.117	.113	.499*	1.000
-.000	-.028	.047	.054	-.022	.042
-.012	-.032	-.014	.095	.052	.098
-.045	-.079	.090	.148	.066	.135
.064	.105	.111	.037	-.033	-.108
.100	.006	.144	.280	.086	.165
.073	.128	-.004	.081	-.032	-.043
-.007	-.075	-.016	.038	-.009	.011
.379	.102	.006	.090	-.032	-.014
-.011	-.089	-.182	-.114	.055	.344

GUW	AIC	M2C	M11
1.000			
.046	1.000		
-.085	-.005	1.000	
-.119	.070	.029	1.000

Table 7. Number of specimens assigned to each population by multiple discriminant analysis of Kinosternon leucostomum males, regression standardized.

Number of Specimens Assigned to Population:

Original Population	A	B	C	D	E	F	G	H	I	J	K	L1	L2	M	N	O	Q	R	S	T	U
A	32	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
B	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
C	0	0	5	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D	0	2	6	33	2	3	2	0	1	0	0	1	0	0	2	0	0	0	1	0	0
E	0	0	2	0	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F	0	0	0	1	0	15	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G	0	0	0	0	1	1	27	0	3	0	0	0	0	0	0	0	0	0	0	0	0
H	0	0	0	0	0	0	0	92	0	0	0	1	1	0	0	0	0	1	0	0	0
I	0	0	0	0	0	0	1	0	14	0	0	1	0	0	0	0	0	0	0	0	0
J	0	0	0	2	3	2	1	0	2	34	8	1	0	0	6	0	0	0	0	6	0
K	0	0	0	0	0	1	0	0	0	6	50	0	1	1	3	0	0	1	1	2	1
L1	0	0	0	0	0	0	0	4	0	0	1	35	11	3	0	2	4	1	1	0	0
L2	0	0	0	0	0	1	0	0	0	1	0	16	57	7	3	3	8	4	0	0	0
M	0	0	0	0	0	0	0	0	0	0	0	2	0	10	0	1	0	2	0	0	0
N	0	0	0	0	0	0	0	0	0	1	1	0	1	0	3	1	0	0	0	0	0

Table 7 (continued)

Number of Specimens Assigned to Population:

Original Population	A	B	C	D	E	F	G	H	R	S	T	U
O	0	0	0	0	0	0	0	0	0	0	0	0
Q	0	0	0	0	0	0	0	0	0	0	0	0
R	0	0	0	0	0	0	0	0	10	0	0	0
S	0	0	0	0	0	0	0	0	0	2	0	0
T	0	0	1	0	0	0	0	0	0	0	9	0
U	0	0	0	0	0	0	0	0	0	0	0	7

I	J	K	L1	L2	M	N	O	Q
0	0	0	0	0	0	0	5	0
0	0	0	0	1	0	0	1	13
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	1	0	0
0	1	1	0	0	0	2	0	0
0	0	0	0	0	0	0	0	0

Table 8. Number of specimens assigned to each population
Kinosternon leucostomum females, regression standardized.

Number of Specimens Assigned to Population:

Original Population	A	B	C	D	E	F	G	H	I
	R	S	T	U					
A	32	0	0	0	1	0	1	0	0
	0	0	0	0					
B	0	4	0	0	0	0	0	0	0
	0	0	0	0					
C	0	0	9	1	0	0	1	0	0
	0	0	0	0					
D	0	0	3	42	6	3	3	0	0
	0	2	0	1					
E	0	0	1	1	10	1	2	0	0
	0	0	0	0					
F	0	0	0	2	0	19	3	0	1
	1	0	0	0					
G	0	0	0	2	4	1	14	0	0
	0	0	0	0					
H	0	0	0	0	1	1	0	38	1
	0	0	0	0					
I	0	0	0	0	0	0	0	0	11
	0	0	0	0					
J	0	0	0	0	0	2	2	0	1
	0	3	1	1					
K	0	0	0	0	0	0	0	0	1
	0	1	0	1					
L1	0	0	0	0	0	0	0	0	1
	1	1	2	0					
L2	0	0	0	0	0	0	0	1	0
	0	0	1	0					
M	0	0	0	0	0	0	0	0	0
	0	0	0	0					
N	0	0	0	0	0	0	0	0	0
	0	0	0	0					

by multiple discriminant analysis of

J	K	L1	L2	M	N	O	Q
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0
1	0	0	2	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1
23	7	0	3	0	7	0	0
5	19	1	1	0	2	0	0
1	0	15	4	4	0	1	0
0	0	1	16	0	0	0	1
0	0	0	0	13	0	0	0
1	0	0	0	0	5	0	2

Table 8 (continued)

Number of Specimens Assigned to Population:

Original Population	A	B	C	D	E	F	G	H	R	S	T	U
O	0	0	0	0	0	0	0	0	0	0	0	0
Q	0	0	0	0	0	0	0	0	0	0	0	1
R	0	0	0	0	0	0	0	0	9	0	0	1
S	0	0	0	0	0	0	0	0	0	5	0	1
T	1	0	0	0	0	0	0	0	0	0	5	1
U	0	0	0	0	0	0	0	0	0	0	0	5

I	J	K	L1	L2	M	N	O	Q
0	0	0	0	0	0	0	1	0
0	0	0	0	1	0	0	0	39
1	0	0	0	0	1	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0

Table 9. Number of specimens assigned to each population by multiple discriminant analysis of Kinosternon leucostomum males, ratio standardized.

Number of Specimens Assigned to Population:

Original Population	A	B	C	D	E	F	G	H	I	J	K	L1	L2	M	N	O	Q	R	S	T	U
A	32	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
B	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C	0	0	5	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D	0	0	5	34	3	3	3	0	1	0	0	1	0	0	2	0	0	0	1	0	0
E	0	0	2	0	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F	0	0	0	0	0	16	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G	0	0	0	0	1	1	27	0	3	0	0	0	0	0	0	0	0	0	0	0	0
H	0	0	0	0	0	0	0	92	0	0	0	1	1	0	0	0	0	1	0	0	0
I	0	0	0	1	0	0	1	0	13	0	0	1	0	0	0	0	0	0	0	0	0
J	0	0	0	1	3	2	1	0	2	33	9	1	0	0	6	0	0	0	0	7	0
K	0	0	0	0	0	1	0	0	0	5	50	0	1	1	4	0	0	1	1	2	1
L1	0	0	0	0	0	0	0	3	1	0	1	36	13	3	0	1	2	1	1	0	0
L2	0	0	0	1	0	0	0	0	0	1	0	19	54	8	3	2	8	4	0	0	0
M	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	2	0	0	0
N	0	0	0	0	0	0	0	0	0	1	1	0	1	0	3	1	0	0	0	0	0

Table 9 (continued)

Number of Specimens Assigned to Population:

Original Population	A	B	C	D	E	F	G	H	R	S	T	U
O	0	0	0	0	0	0	0	0	0	0	0	0
Q	0	0	0	0	0	0	0	0	0	0	0	0
R	0	0	0	0	0	0	0	0	10	0	0	0
S	0	0	0	0	0	0	0	0	0	2	0	0
T	0	0	1	0	0	0	0	0	0	0	9	0
U	0	0	0	0	0	0	0	0	0	0	0	7

I	J	K	L1	L2	M	N	O	Q
0	0	0	0	0	0	0	5	0
0	0	0	0	1	0	0	1	13
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	1	0	0
0	1	1	0	0	0	2	0	0
0	0	0	0	0	0	0	0	0

Table 10. Number of specimens assigned to each population by multiple discriminant analysis of <u>Kinosternon leucostomum</u> females, ratio standardized.

Number of Specimens Assigned to Population:

Original Population	A	B	C	D	E	F	G	H	I	J	K	L1	L2	M	N	O	Q	R	S	T	U
A	32	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C	0	0	8	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
D	0	0	3	46	5	2	2	1	0	1	0	0	1	0	0	0	0	0	1	0	1
E	0	0	1	1	10	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F	0	0	0	1	0	21	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0
G	0	0	0	2	4	1	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H	0	0	0	0	1	1	1	37	1	0	0	0	0	0	0	0	0	0	0	0	0
I	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0
J	0	0	0	0	0	2	2	0	1	22	8	0	3	0	7	0	0	0	3	1	1
K	0	0	0	0	0	0	0	0	1	4	20	1	1	0	2	0	0	0	1	0	1
L1	0	0	0	0	0	0	0	0	1	1	0	14	4	4	0	1	0	2	1	2	0
L2	0	0	0	0	0	0	0	1	0	0	0	1	16	0	0	0	1	0	0	1	0
M	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0
N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5	0	2	0	0	0	0

Table 10 (continued)

Original Population	Number of Specimens Assigned to Population: A	B	C	D	E	F	G	H	R	S	T	U
O	0	0	0	0	0	0	0	0	0	0	0	0
Q	0	0	0	0	0	0	0	0	0	0	0	3
R	0	0	0	0	0	0	0	0	9	0	0	1
S	0	0	0	0	0	0	0	0	0	6	0	0
T	1	0	0	0	0	0	0	0	0	0	6	0
U	0	0	0	0	0	0	0	0	0	0	0	5

I	J	K	L1	L2	M	N	O	Q
0	0	0	0	0	0	0	1	0
0	0	0	0	2	0	0	0	36
1	0	0	0	0	1	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0

Table 11. Summary table of multiple discriminant analysis of *Kinosternon leucostomum* males, regression standardized.

Step	Variable Selected	F Value
1	TFW	38.931
2	SHT	30.943
3	ABL	24.624
4	CWP	16.692
5	GUL	10.959
6	INL	7.033
7	PHW	6.778
8	AHW	6.633
9	CWN	6.624
10	ANL	5.883
11	FEL	5.343
12	PEL	4.883
13	BRL	4.690
14	GUW	4.366
15	AIC	4.130
16	AXL	4.179
17	HW	4.405
18	C3W	3.752
19	C1A	3.633
20	C1P	3.082
21	C5W	2.981
22	HUL	2.633
23	HPW	2.424
24	M2C	2.187
25	M11	1.939
26	CWA	1.737
27	C5L	1.658
28	CWN	1.487
29	C3L	1.425
30	C1L	1.405
31	FAW	.964

Table 12. Summary table of multiple discriminant analysis of *Kinosternon leucostomum* females, regression standardized.

Step	Variable Selected	F Value
1	SHT	30.362
2	ABL	22.635
3	C1L	12.213
4	AHW	8.391
5	CWA	9.879
6	INL	7.636
7	PHW	6.831
8	HW	5.931
9	BRL	5.938
10	C3W	4.665
11	GUL	4.617
12	AIC	4.628
13	CWN	3.902
14	GUW	3.437
15	AXL	3.195
16	PEL	2.728
17	CWP	2.709
18	C5W	2.622
19	TFW	2.678
20	FEL	2.608
21	ANL	2.089
22	HPW	2.340
23	C3L	2.291
24	HUL	1.857
25	FAW	1.815
26	M11	1.740
27	C5L	1.833
28	M2C	1.395
29	C1A	1.168
30	SIM	1.076
31	C1P	1.019

Table 13. Summary table of multiple discriminant analysis of *Kinosternon leucostomum* males, ratio standardized.

Step	Variable Selected	F Value
1	TFW	40.325
2	SHT	28.737
3	ABL	26.698
4	CWP	18.349
5	GUL	11.417
6	INL	7.413
7	PHW	6.621
8	ANL	6.542
9	AHW	6.577
10	FEL	6.327
11	CWN	5.918
12	PEL	5.278
13	AXL	4.965
14	AIC	5.049
15	HW	4.993
16	BRL	4.419
17	C3W	3.999
18	HUL	3.808
19	C1A	3.694
20	C1P	3.231
21	C5W	3.461
22	GUW	2.783
23	HPW	2.740
24	M2C	2.139
25	M11	1.871
26	C5L	1.838
27	CWA	1.640
28	C1L	1.574
29	C3L	1.567
30	SIM	1.320
31	FAW	.944

Table 14. Summary table of multiple discriminant analysis of *Kinosternon leucostomum* females, ratio standardized.

Step	Variable Selected	F Value
1	SHT	30.028
2	ABL	23.821
3	C1L	12.947
4	INL	8.190
5	AHW	7.620
6	CWA	9.686
7	PHW	6.978
8	HW	6.002
9	BRL	6.202
10	AIC	4.913
11	C3W	4.752
12	GUL	4.738
13	CWN	3.660
14	GUW	3.554
15	AXL	3.168
16	FEL	2.670
17	ANL	4.579
18	TFW	2.649
19	CWP	2.890
20	PEL	2.599
21	C3L	2.246
22	C5W	2.364
23	HPW	2.339
24	HUL	1.992
25	FAW	1.784
26	M11	1.704
27	C5L	1.901
28	M2C	1.380
29	CiA	1.171
30	SIM	1.013
31	C1P	1.011

Table 15. Mean values of each character for each population of *Kinosternon leucostomum* males, expressed as a proportion of CL except as described in the text.

Character	Population A	B	C	D	E	F	G	H	I	J	K
CWN	6.270	6.750	6.571	6.245	6.230	6.176	5.968	7.200	6.562	6.738	6.507
CWA	.628	.626	.609	.611	.607	.620	.606	.615	.604	.607	.605
CWP	.629	.634	.612	.614	.605	.618	.601	.626	.607	.619	.612
ABL	.208	.207	.216	.208	.209	.202	.210	.203	.216	.228	.239
AHW	.466	.471	.447	.448	.441	.446	.441	.426	.421	.445	.440
PHW	.382	.393	.387	.383	.382	.375	.361	.369	.353	.387	.373
TFW	.412	.430	.437	.428	.427	.427	.416	.395	.404	.435	.429
GUL	.139	.142	.145	.145	.138	.153	.153	.134	.143	.123	.121
HUL	.143	.167	.142	.135	.136	.127	.138	.141	.129	.151	.150
PEL	.050	.041	.042	.043	.046	.041	.028	.038	.040	.037	.032
FEL	.060	.058	.058	.071	.071	.072	.064	.069	.067	.061	.059
ANL	.278	.289	.302	.285	.281	.283	.290	.279	.271	.278	.277
SHT	.412	.412	.390	.373	.364	.370	.377	.344	.353	.366	.366
BRL	.238	.241	.239	.245	.242	.238	.251	.230	.250	.242	.252
HW	.205	.213	.199	.191	.196	.199	.197	.195	.184	.185	.182
C1L	.222	.217	.206	.209	.201	.206	.211	.209	.197	.215	.212
C1A	.223	.224	.208	.220	.222	.233	.224	.225	.218	.229	.230
C1P	.043	.051	.044	.047	.046	.043	.036	.045	.045	.047	.045
C3L	.210	.214	.212	.213	.205	.209	.206	.196	.210	.207	.209
C3W	.221	.239	.228	.233	.219	.220	.210	.220	.209	.218	.215
C5L	.201	.201	.195	.189	.191	.191	.198	.192	.194	.192	.189
C5W	.200	.218	.201	.191	.198	.203	.181	.177	.183	.198	.192
SIM	.081	.125	.000	.037	.000	.058	.000	.263	.187	.030	.014
AXL	.202	.192	.192	.199	.191	.201	.193	.177	.161	.192	.192
INL	.240	.238	.251	.252	.243	.240	.228	.230	.214	.241	.244
HPW	.376	.383	.362	.359	.361	.355	.363	.335	.350	.358	.355
FAW	.316	.323	.327	.322	.330	.332	.317	.313	.316	.329	.326
GUW	.179	.181	.163	.165	.171	.173	.168	.174	.163	.161	.151
AIC	1.540	.500	.714	.641	.769	.352	.281	.221	.000	.415	.268
M2C	1.675	1.250	1.714	1.660	1.923	1.882	1.937	1.926	2.000	1.984	1.955
M11	.756	.875	.714	.320	.692	.764	.375	.378	.125	.492	.820

Table 15 (continued)

	Population				
	L1	L2	M	N	O
Character					
CWN	6.096	5.980	6.066	6.142	6.600
CWA	.615	.619	.611	.609	.618
CWP	.619	.619	.612	.608	.633
ABL	.226	.218	.222	.224	.218
AHW	.420	.421	.405	.439	.408
PHW	.366	.368	.351	.384	.361
TFW	.397	.393	.383	.421	.381
GUL	.119	.117	.122	.119	.104
HUL	.137	.140	.129	.143	.117
PEL	.040	.043	.038	.049	.060
FEL	.056	.061	.067	.063	.060
ANL	.256	.253	.247	.275	.247
SHT	.354	.357	.353	.366	.359
BRL	.231	.228	.237	.240	.227
HW	.165	.186	.185	.183	.188
C1L	.208	.210	.195	.217	.213
C1A	.216	.228	.214	.227	.238
C1P	.046	.049	.042	.050	.046
C3L	.202	.207	.202	.212	.208
C3W	.222	.224	.217	.223	.222
C5L	.168	.191	.203	.185	.190
C5W	.194	.200	.194	.200	.207
SIM	.032	.020	.000	.000	.000
AXL	.187	.190	.201	.181	.192
INL	.230	.217	.240	.240	.239
HPW	.340	.336	.334	.354	.323
FAW	.314	.312	.299	.332	.310
GUW	.155	.157	.150	.156	.145
AIC	.177	.130	.200	.000	.800
M2C	1.709	1.600	1.800	1.571	1.800
M11	.677	1.090	1.066	.285	.800

Q	R	S	T	U	Overall Means
6.133	6.500	5.750	6.285	7.428	6.419
.614	.623	.620	.612	.638	.614
.618	.625	.617	.624	.661	.619
.218	.222	.229	.234	.231	.218
.424	.427	.449	.450	.458	.435
.374	.364	.376	.390	.410	.373
.387	.392	.424	.435	.442	.411
.118	.128	.122	.112	.116	.129
.141	.125	.150	.138	.137	.141
.048	.044	.044	.057	.061	.041
.069	.070	.050	.065	.054	.063
.252	.259	.279	.278	.293	.272
.361	.371	.386	.374	.375	.365
.220	.233	.243	.244	.244	.238
.191	.190	.203	.194	.181	.190
.224	.209	.210	.218	.212	.211
.217	.228	.214	.214	.218	.224
.048	.046	.054	.048	.048	.046
.204	.216	.218	.219	.207	.206
.209	.222	.233	.226	.219	.221
.190	.195	.192	.195	.171	.192
.197	.200	.195	.210	.195	.193
.066	.000	.000	.000	.000	.066
.179	.206	.203	.191	.201	.190
.214	.245	.262	.254	.223	.234
.334	.338	.363	.361	.356	.349
.306	.314	.327	.327	.330	.318
.160	.148	.163	.150	.155	.162
.000	1.100	1.000	.357	.142	.374
1.333	1.800	1.750	1.714	1.285	1.782
.266	1.500	.500	.714	.000	.647

Table 16. Mean values of each character for each population of Kinosternon leucostomum females, expressed as a proportion of CL except as described in the text.

Character	Population A	B	C	D	E	F	G	H	I	J	K
CWN	6.029	6.250	6.250	6.206	6.133	6.461	6.095	6.975	7.083	6.280	6.387
CWA	.636	.641	.638	.627	.633	.627	.622	.622	.620	.614	.614
CWP	.633	.632	.633	.631	.632	.625	.623	.633	.633	.623	.621
ABL	.215	.196	.216	.214	.208	.213	.211	.205	.217	.232	.240
AHW	.477	.489	.468	.463	.458	.446	.449	.431	.427	.454	.458
PHW	.403	.402	.413	.404	.405	.380	.385	.367	.374	.398	.392
TFW	.439	.437	.455	.444	.449	.427	.438	.409	.415	.442	.436
GUL	.133	.151	.142	.143	.139	.152	.150	.130	.122	.118	.115
HUL	.164	.163	.148	.145	.148	.137	.144	.143	.143	.161	.163
PEL	.047	.020	.035	.039	.036	.030	.030	.036	.039	.033	.028
FEL	.049	.053	.055	.065	.067	.070	.064	.067	.070	.061	.056
ANL	.312	.321	.322	.311	.301	.294	.311	.290	.278	.292	.300
SHT	.449	.453	.411	.406	.394	.388	.398	.348	.355	.378	.381
BRL	.256	.249	.260	.249	.260	.255	.263	.252	.239	.247	.253
HW	.199	.203	.196	.187	.192	.184	.190	.186	.181	.176	.174
C1L	.230	.232	.209	.209	.208	.203	.206	.207	.211	.214	.207
C1A	.227	.254	.232	.222	.226	.218	.228	.221	.223	.228	.228
C1P	.048	.051	.046	.048	.046	.042	.043	.046	.051	.047	.047
C3L	.224	.212	.221	.219	.220	.218	.214	.198	.207	.211	.213
C3W	.233	.252	.231	.243	.233	.215	.222	.227	.216	.224	.218
C5L	.178	.185	.176	.171	.170	.170	.165	.175	.170	.165	.166
C5W	.191	.210	.191	.180	.185	.184	.176	.178	.178	.184	.184
SIM	.088	.000	.166	.095	.000	.230	.000	.097	.166	.060	.000
AXL	.202	.173	.186	.195	.182	.199	.188	.177	.182	.188	.182
INL	.253	.252	.252	.262	.241	.251	.238	.240	.223	.247	.250
HPW	.382	.393	.369	.362	.361	.359	.362	.339	.349	.357	.359
FAW	.322	.335	.334	.328	.333	.324	.329	.317	.320	.329	.328
GUW	.177	.174	.165	.167	.167	.175	.173	.166	.160	.160	.147
AIC	1.588	.750	.333	.460	.266	.461	.190	.439	.000	.300	.000
M2C	1.735	2.000	2.000	1.746	1.866	1.692	1.952	1.780	1.916	1.920	2.000
MII	.411	.750	.166	.158	.333	.230	.238	.560	.000	.200	.387

Table 16 (continued)

Character	Population L1	L2	M	N	O
CWN	6.233	6.200	6.230	6.250	7.000
CWA	.630	.626	.625	.605	.634
CWP	.639	.636	.629	.606	.627
ABL	.237	.228	.236	.228	.222
AHW	.442	.440	.414	.459	.436
PHW	.393	.394	.374	.407	.396
TFW	.430	.427	.411	.440	.420
GUL	.117	.115	.116	.120	.134
HUL	.147	.156	.137	.165	.127
PEL	.038	.034	.032	.031	.031
FEL	.058	.061	.059	.069	.063
ANL	.287	.293	.293	.298	.293
SHT	.387	.390	.391	.390	.404
BRL	.250	.244	.248	.249	.246
HW	.179	.178	.178	.174	.182
C1L	.208	.216	.194	.222	.222
C1A	.220	.233	.208	.235	.222
C1P	.047	.050	.042	.048	.047
C3L	.217	.213	.216	.219	.214
C3W	.231	.225	.220	.217	.230
C5L	.168	.162	.176	.161	.166
C5W	.196	.189	.194	.174	.198
SIM	.000	.000	.000	.000	.000
AXL	.189	.179	.200	.177	.182
INL	.240	.225	.253	.237	.254
HPW	.352	.346	.345	.363	.357
FAW	.329	.316	.314	.328	.325
GUW	.153	.160	.150	.156	.158
AIC	.133	.000	.307	.000	.000
M2C	1.400	1.450	1.769	2.000	2.000
M11	.666	.650	.923	.000	.000

Q	R	S	T	U	Overall Means
6,121	6,083	6,142	6,142	6.168	6,306
,642	,640	,615	.621	.624	.626
,643	,641	,612	.617	.620	.630
,226	,234	,231	,243	.239	.222
,457	,442	,454	,457	,451	,452
,410	,384	,392	,396	,397	,394
,435	,422	,440	,445	,436	,434
,116	,127	,119	,115	.119	.128
,158	,134	,157	,142	,142	.151
,044	,050	,031	,050	,042	,037
,075	,054	,054	,061	,063	,063
,291	,294	,304	,280	,287	,298
,395	,383	,411	,391	,387	,392
,237	,251	,246	,255	,255	,250
,184	,182	,185	,181	,184	,184
,244	,205	,214	,215	,216	,214
,233	,220	,219	,211	,228	,225
,058	,049	,045	,049	,047	,048
,217	,222	,220	,221	,212	,215
,216	,225	,219	,232	,219	,227
,156	,176	,171	,180	,159	,169
,173	,189	,188	,203	,182	,184
,024	,000	,142	,000	,000	,061
,180	,195	,187	,184	,189	,188
,213	,241	,267	,260	,256	,244
,361	,348	,368	,359	,368	,358
,314	,336	,333	,333	,323	,325
,156	,143	,144	,149	,153	,162
,000	,083	,285	,285	,333	,348
1,365	2,000	1,714	1,857	1,666	1,751
,048	,166	,714	1,142	,333	,339

Table 17. Standard deviations of each character for males.

	Population				
	A	B	C	D	E
Character					
CWN	1.017	1.388	1.133	.806	1.091
CWA	.017	.012	.016	.019	.017
CWP	.021	.020	.017	.022	.021
ABL	.015	.012	.008	.013	.010
AHW	.018	.010	.011	.016	.013
PHW	.015	.014	.017	.019	.012
TFW	.017	.008	.012	.013	.013
GUL	.013	.011	.018	.015	.020
HUL	.018	.011	.016	.018	.019
PEL	.014	.014	.016	.014	.016
FEL	.015	.014	.008	.013	.013
ANL	.019	.019	.013	.019	.012
SHT	.019	.029	.017	.019	.019
BRL	.008	.006	.014	.014	.011
HW	.011	.011	.008	.009	.013
C1L	.016	.013	.016	.018	.015
C1A	.019	.023	.017	.020	.019
C1P	.006	.005	.011	.009	.010
C3L	.011	.006	.009	.012	.011
C3W	.018	.015	.016	.017	.011
C5L	.010	.015	.013	.014	.012
C5W	.020	.027	.011	.021	.018
SIM	.363	.353	.000	.192	.000
AXL	.016	.012	.019	.015	.009
INL	.011	.016	.015	.016	.023
HPW	.014	.011	.008	.016	.012
FAW	.014	.007	.020	.015	.011
GUW	.016	.016	.018	.014	.017
AIC	.836	.925	.951	.879	.926
M2C	.709	1.035	.487	.732	.277
M11	.925	.834	.951	.613	.854

each population of <u>Kinosternon leucostomum</u>

F	G	H	I	J	K
1.074	.966	.906	1.152	1.004	.943
.020	.016	.013	.018	.015	.019
.027	.019	.014	.023	.017	.022
.012	.009	.010	.007	.011	.014
.016	.013	.014	.014	.016	.020
.015	.013	.016	.014	.017	.020
.014	.016	.012	.012	.016	.018
.015	.013	.011	.014	.018	.014
.016	.015	.014	.017	.019	.017
.013	.012	.011	.015	.014	.015
.015	.014	.010	.011	.015	.012
.010	.012	.012	.015	.016	.021
.015	.017	.013	.018	.016	.015
.011	.013	.016	.007	.014	.014
.006	.008	.007	.006	.009	.013
.020	.011	.015	.016	.017	.015
.019	.019	.014	.019	.017	.019
.008	.005	.006	.009	.006	.006
.012	.013	.017	.008	.015	.011
.018	.011	.014	.012	.013	.015
.014	.009	.012	.012	.017	.014
.018	.017	.018	.026	.023	.016
.242	.000	.530	.543	.248	.122
.016	.016	.015	.015	.014	.016
.018	.018	.016	.025	.022	.019
.019	.011	.016	.014	.014	.016
.013	.019	.011	.009	.013	.018
.012	.011	.012	.012	.015	.016
.701	.634	.604	.000	.768	.687
.485	.353	.333	.000	.124	.208
.970	.659	.717	.341	.831	.903

Table 17 (continued)

Character	Population L1	L2	M	N	O	Q	R	S	T	U
CWN	.803	.803	.457	.690	.547	.743	.849	.500	.994	.766
CWA	.016	.015	.020	.029	.012	.018	.029	.030	.016	.035
CWP	.020	.016	.021	.030	.011	.019	.029	.019	.012	.024
ABL	.012	.010	.012	.010	.007	.009	.010	.016	.012	.012
AHW	.021	.013	.019	.009	.013	.018	.026	.010	.015	.024
PHW	.016	.013	.013	.008	.009	.013	.023	.019	.013	.029
TFW	.015	.014	.020	.021	.016	.018	.020	.020	.014	.027
GUL	.015	.015	.012	.015	.023	.018	.016	.022	.021	.011
HUL	.018	.019	.014	.027	.012	.020	.020	.019	.013	.028
PEL	.012	.011	.007	.012	.006	.013	.011	.014	.013	.012
FEL	.016	.012	.012	.008	.003	.011	.025	.008	.023	.010
ANL	.023	.016	.013	.009	.011	.014	.013	.007	.016	.021
SHT	.014	.015	.019	.003	.001	.013	.014	.018	.016	.025
BRL	.009	.009	.011	.017	.004	.010	.005	.007	.019	.015
HW	.010	.008	.012	.008	.007	.005	.011	.006	.014	.010
C1L	.023	.012	.015	.008	.009	.013	.010	.011	.012	.012
C1A	.026	.017	.018	.021	.011	.014	.025	.010	.018	.014
C1P	.010	.007	.009	.009	.009	.008	.009	.009	.007	.067
C3L	.020	.011	.010	.010	.013	.007	.008	.010	.012	.012
C3W	.021	.016	.008	.016	.011	.021	.022	.020	.011	.013
C5L	.019	.014	.012	.014	.010	.015	.010	.011	.009	.013
C5W	.030	.020	.026	.013	.009	.018	.014	.006	.009	.009
SIM	.178	.200	.000	.000	.000	.258	.000	.000	.000	.000
AXL	.012	.012	.011	.002	.010	.012	.012	.011	.011	.022
INL	.021	.024	.016	.009	.015	.017	.009	.015	.015	.039
HPW	.017	.014	.018	.008	.019	.012	.015	.013	.015	.024
FAW	.014	.015	.036	.013	.005	.017	.019	.010	.011	.030
GUW	.014	.013	.017	.016	.027	.011	.015	.010	.015	.020
AIC	.558	.485	.560	.000	1.095	.000	.994	1.154	.744	.377
M2C	.662	.752	.560	.786	.447	.975	.632	.500	.611	.755
M11	.864	.933	.961	.755	1.095	.703	.849	1.000	.825	.000

Table 18. Standard deviations of each character for females.

Character	A	B	C	D	E
CWN	.300	.500	.452	.572	.351
CWA	.021	.019	.022	.019	.017
CWP	.021	.025	.017	.021	.029
ABL	.010	.005	.012	.011	.015
AHW	.018	.016	.021	.015	.011
PHW	.017	.017	.018	.014	.024
TFW	.019	.007	.015	.015	.017
GUL	.012	.010	.013	.015	.016
HUL	.016	.017	.017	.018	.013
PEL	.015	.008	.015	.015	.014
FEL	.013	.014	.013	.014	.020
ANL	.017	.015	.017	.023	.027
SHT	.027	.028	.022	.024	.015
BRL	.008	.005	.013	.014	.017
HW	.008	.007	.006	.009	.008
C1L	.021	.015	.009	.014	.021
C1A	.021	.021	.013	.019	.023
C1P	.009	.004	.009	.008	.010
C3L	.015	.010	.010	.012	.010
C3W	.016	.007	.018	.023	.021
C5L	.015	.007	.015	.011	.011
C5W	.021	.005	.019	.017	.015
SIM	.378	.000	.389	.346	.000
AXL	.012	.043	.017	.015	.018
INL	.019	.017	.022	.019	.022
HPW	.015	.021	.011	.014	.016
FAW	.021	.026	.016	.018	.014
GUW	.015	.022	.019	.014	.015
AIC	.988	.957	.778	.819	.703
M2C	.898	.000	.000	.621	.516
M11	.783	.957	.577	.514	.723

Population: A, B, C, D, E

each population of Kinosternon leucostomum

F	G	H	I	J	K
.904	.538	.792	.569	.607	.715
.022	.016	.027	.016	.016	.016
.023	.014	.034	.018	.018	.018
.008	.009	.008	.009	.012	.010
.018	.014	.014	.015	.015	.017
.014	.012	.025	.015	.019	.018
.018	.014	.011	.015	.018	.025
.015	.016	.017	.014	.018	.011
.015	.016	.016	.021	.019	.014
.015	.016	.011	.011	.012	.016
.018	.015	.014	.011	.012	.009
.024	.018	.021	.013	.016	.016
.016	.015	.016	.016	.018	.017
.013	.016	.014	.012	.014	.012
.013	.005	.009	.006	.008	.006
.017	.009	.021	.013	.014	.015
.024	.018	.023	.017	.019	.016
.007	.009	.007	.007	.009	.007
.010	.011	.009	.017	.010	.011
.018	.013	.018	.011	.017	.014
.011	.010	.012	.014	.012	.015
.018	.016	.015	.019	.013	.017
.514	.000	.389	.374	.239	.000
.016	.018	.015	.017	.013	.018
.018	.021	.023	.019	.021	.019
.016	.012	.011	.014	.015	.015
.020	.013	.011	.012	.019	.026
.014	.010	.018	.011	.017	.014
.760	.601	.000	.838	.707	.000
.679	.218	.288	.570	.340	.000
.514	.624	.000	.807	.571	.715

Table 18 (continued)

Character	Population L1	L2	M	N	O
CWN	.568	.695	.599	.462	.000
CWA	.016	.015	.016	.019	.000
CWP	.018	.016	.016	.021	.000
ABL	.016	.014	.009	.013	.000
AHW	.017	.017	.015	.010	.000
PHW	.016	.014	.012	.011	.000
TFW	.016	.014	.013	.017	.000
GUL	.015	.013	.019	.008	.000
HUL	.015	.017	.018	.025	.000
PEL	.014	.012	.008	.019	.000
FEL	.015	.017	.015	.013	.000
ANL	.019	.016	.016	.010	.000
SHT	.022	.018	.019	.020	.000
BRL	.011	.009	.011	.022	.000
HW	.008	.008	.009	.012	.000
C1L	.012	.013	.013	.010	.000
C1A	.018	.020	.023	.017	.000
C1P	.007	.007	.007	.005	.000
C3L	.009	.010	.010	.009	.000
C3W	.018	.011	.015	.015	.000
C5L	.012	.010	.010	.020	.000
C5W	.020	.020	.022	.017	.000
SIM	.000	.000	.000	.000	.000
AXL	.019	.010	.011	.009	.000
INL	.027	.021	.023	.015	.000
HPW	.012	.012	.013	.012	.000
FAW	.015	.019	.012	.013	.000
GUW	.014	.013	.013	.010	.000
AIC	.507	.000	.630	.000	.000
M2C	.855	.887	.599	.000	.000
M11	.884	.812	1.037	.000	.000

Q	R	S	T	U
.399	.900	.377	.377	.752
.017	.023	.007	.011	.018
.018	.032	.009	.008	.028
.008	.017	.011	.013	.016
.014	.019	.015	.008	.026
.016	.021	.016	.012	.026
.016	.032	.006	.012	.023
.016	.053	.012	.018	.011
.015	.037	.012	.016	.012
.011	.015	.017	.012	.012
.015	.013	.023	.012	.020
.018	.027	.022	.015	.030
.016	.024	.031	.034	.026
.009	.021	.012	.018	.019
.006	.008	.006	.008	.014
.017	.018	.021	.012	.011
.017	.015	.020	.010	.021
.008	.008	.008	.004	.012
.014	.011	.010	.016	.011
.018	.015	.015	.013	.016
.014	.025	.005	.012	.011
.019	.020	.018	.012	.017
.156	.000	.377	.000	.000
.010	.015	.015	.013	.025
.018	.027	.018	.014	.007
.016	.016	.007	.015	.020
.016	.014	.018	.019	.019
.016	.024	.011	.016	.023
.000	.288	.755	.487	.516
.915	.000	.487	.377	.516
.312	.389	.951	1.069	.516

Table 19. Mean values of each character for each population as a proportion of CL except as described in the text.

	Population					
	1A	1B	2	3	4	5
Character						
CWN	6.923	7.000	7.192	7.090	7.137	6.750
CWA	.606	.606	.629	.612	.603	.588
CWP	.628	.625	.649	.624	.630	.612
ABL	.287	.263	.269	.261	.260	.261
AHW	.477	.468	.492	.479	.459	.465
PHW	.403	.407	.421	.396	.398	.386
TFW	.443	.445	.452	.436	.429	.421
GUL	.162	.148	.150	.157	.148	.143
HUL	.097	.104	.127	.124	.122	.125
PEL	.033	.071	.057	.044	.051	.044
FEL	.077	.076	.084	.092	.096	.077
ANL	.228	.236	.230	.226	.207	.206
SHT	.352	.369	.377	.365	.350	.355
BRL	.276	.243	.245	.234	.238	.249
HW	.188	.202	.206	.206	.195	.192
C1L	.206	.214	.214	.223	.200	.194
C1A	.182	.212	.222	.224	.209	.194
C1P	.055	.070	.070	.063	.072	.062
C3L	.209	.215	.220	.224	.219	.227
C3W	.195	.211	.218	.216	.220	.211
C5L	.200	.200	.199	.197	.191	.197
C5W	.249	.226	.229	.223	.221	.227
DKL	.230	.692	.730	.878	.724	1.000
DKC	.307	1.076	1.076	1.090	1.206	1.000
SIM	.000	.384	.615	.363	.241	.250
AXL	.101	.141	.145	.142	.144	.137
INL	.195	.267	.257	.256	.255	.259
NOT	.026	.023	.030	.019	.029	.044
HPW	.372	.377	.389	.375	.376	.376
FAW	.328	.341	.345	.318	.315	.325
GUW	.191	.182	.189	.181	.172	.167
AIC	.000	.769	1.346	.787	1.448	1.000
M2C	.307	1.538	1.423	1.727	1.344	1.000
M11	2.000	1.923	1.923	1.121	1.379	2.000

of Kinosternon integrum males, expressed

6	7	8A	8B	9A
7.058	7.375	6.800	7.000	7.000
.596	.612	.608	.634	.617
.620	.635	.634	.648	.638
.261	.255	.256	.234	.259
.452	.468	.474	.417	.484
.396	.410	.410	.357	.410
.423	.434	.438	.373	.446
.150	.157	.152	.141	.160
.117	.112	.120	.101	.119
.052	.056	.051	.041	.047
.084	.085	.066	.117	.080
.205	.209	.223	.176	.217
.364	.373	.372	.364	.369
.240	.235	.242	.188	.243
.199	.207	.199	.217	.200
.198	.209	.203	.232	.214
.203	.225	.209	.222	.229
.065	.068	.059	.053	.062
.224	.219	.220	.209	.216
.222	.219	.216	.219	.221
.192	.198	.191	.195	.190
.218	.229	.225	.224	.230
.470	.750	.800	.500	1.000
.882	1.000	1.200	.500	1.166
.294	.208	.000	.000	.222
.135	.140	.146	.144	.154
.241	.254	.252	.229	.258
.029	.030	.033	.036	.031
.363	.393	.378	.360	.393
.312	.327	.324	.301	.324
.173	.179	.180	.188	.190
1.235	.875	1.500	2.000	1.055
1.823	1.700	1.600	1.000	1.722
1.823	2.000	2.000	2.000	2.000

Table 19 (continued)

	Population				
	9B	10	11A	11B	12
Character					
CWN	6.750	7.357	6.857	6.500	7.111
CWA	.618	.611	.622	.653	.607
CWP	.633	.629	.645	.670	.634
ABL	.266	.261	.257	.251	.249
AHW	.487	.438	.490	.508	.484
PHW	.418	.386	.412	.438	.415
TFW	.447	.416	.452	.455	.433
GUL	.164	.154	.159	.170	.144
HUL	.122	.104	.131	.114	.127
PEL	.049	.049	.039	.044	.058
FEL	.083	.088	.068	.072	.070
ANL	.224	.198	.234	.244	.217
SHT	.384	.352	.364	.371	.370
BRL	.244	.225	.252	.235	.227
HW	.179	.207	.197	.197	.209
C1L	.214	.208	.211	.216	.200
C1A	.209	.208	.228	.255	.224
C1P	.068	.060	.061	.064	.068
C3L	.214	.216	.213	.209	.221
C3W	.221	.210	.218	.234	.219
C5L	.175	.192	.188	.181	.186
C5W	.196	.213	.230	.222	.231
DKL	1.375	.857	.714	1.100	.444
DKC	1.625	1.250	1.142	1.600	.555
SIM	.250	.142	.000	.200	.333
AXL	.139	.164	.126	.151	.149
INL	.253	.232	.250	.275	.250
NOT	.029	.035	.034	.025	.029
HPW	.386	.361	.393	.414	.400
FAW	.321	.326	.334	.327	.320
GUW	.186	.184	.181	.188	.186
AIC	.750	1.714	.285	1.400	.888
M2C	1.000	.714	1.571	1.900	1.666
MII	1.750	1.928	2.000	2.000	1.666

13	14	15	16	17	18
7.384	7.148	7.230	6.500	7.300	6.900
.600	.611	.587	.602	.596	.617
.623	.636	.615	.619	.626	.647
.252	.274	.272	.256	.256	.260
.466	.445	.452	.432	.462	.474
.385	.403	.394	.365	.398	.412
.423	.437	.437	.393	.433	.445
.150	.159	.147	.148	.160	.182
.120	.118	.117	.101	.122	.106
.048	.044	.037	.051	.037	.051
.084	.079	.063	.092	.081	.084
.211	.216	.225	.190	.203	.222
.354	.345	.349	.347	.349	.364
.236	.240	.240	.220	.233	.231
.193	.202	.202	.204	.206	.206
.210	.207	.197	.204	.205	.202
.226	.231	.220	.221	.223	.219
.061	.055	.055	.055	.063	.069
.215	.212	.207	.215	.205	.214
.213	.198	.193	.194	.204	.220
.197	.192	.196	.198	.195	.190
.229	.210	.211	.216	.227	.225
1.230	1.407	1.384	1.833	1.100	1.000
1.230	1.925	1.615	1.944	1.400	1.600
.076	.222	.307	.055	.000	.100
.150	.167	.157	.159	.146	.139
.248	.242	.235	.237	.249	.252
.033	.026	.034	.038	.040	.028
.387	.363	.352	.352	.381	.386
.320	.332	.334	.307	.337	.330
.190	.181	.175	.169	.170	.186
.692	1.592	1.384	1.611	1.100	.900
1.846	1.555	1.692	1.555	1.700	1.600
1.846	2.000	2.000	1.888	1.900	2.000

Table 19 (continued)

	Population	
	19	20A
Character		
CWN	7.833	7.500
CWA	.595	.611
CWP	.637	.651
ABL	.263	.261
AHW	.472	.440
PHW	.411	.417
TFW	.440	.452
GUL	.164	.156
HUL	.093	.099
PEL	.059	.058
FEL	.077	.094
ANL	.232	.203
SHT	.372	.360
BRL	.229	.229
HW	.202	.211
C1L	.201	.207
C1A	.221	.216
C1P	.069	.069
C3L	.221	.203
C3W	.206	.203
C5L	.191	.203
C5W	.217	.228
DKL	1.333	1.000
DKC	1.583	1.500
SIM	.000	.000
AXL	.148	.145
INL	.257	.250
NOT	.024	.027
HPW	.389	.354
FAW	.317	.336
GUW	.191	.178
AIC	.000	2.000
M2C	1.666	1.000
M11	2.000	2.000

208	Overall Means
7.666	7.108
.600	.610
.632	.632
.256	.262
.410	.466
.347	.401
.369	.433
.149	.155
.095	.115
.035	.049
.091	.083
.188	.216
.341	.361
.221	.237
.204	.201
.199	.208
.226	.219
.056	.063
.208	.217
.180	.212
.199	.194
.217	.222
3.333	.966
3.333	1.272
.000	.220
.145	.146
.243	.248
.056	.030
.345	.377
.302	.325
.175	.181
2.000	1.125
2.000	1.481
2.000	1.818

Table 20. Mean values of each character for each population of Kinosternon integrum females, expressed as a proportion of CL except as described in the text.

	Population										
Character	1A	1B	2	3	4	5	6	7	8A	8B	9A
CWN	6.800	6.703	6.933	6.484	6.735	6.285	6.555	6.900	6.166	8.000	6.166
CWA	.628	.630	.631	.626	.628	.635	.626	.644	.631	.622	.662
CWP	.651	.644	.654	.639	.656	.654	.646	.666	.650	.660	.669
ABL	.315	.271	.270	.277	.275	.281	.274	.280	.272	.235	.270
AHW	.500	.489	.496	.493	.404	.485	.478	.507	.487	.434	.527
PHW	.438	.433	.433	.423	.429	.440	.430	.447	.434	.386	.456
TFW	.476	.467	.461	.459	.449	.466	.457	.478	.458	.415	.480
GUL	.159	.161	.152	.160	.151	.163	.146	.163	.157	.132	.169
HUL	.104	.106	.122	.119	.131	.116	.137	.113	.122	.094	.129
PEL	.032	.065	.056	.046	.047	.053	.048	.043	.050	.056	.050
FEL	.081	.069	.068	.077	.085	.071	.078	.067	.065	.122	.070
ANL	.256	.265	.257	.256	.241	.258	.233	.261	.255	.207	.259
SHT	.406	.382	.391	.392	.380	.406	.412	.392	.390	.358	.393
BRL	.300	.252	.246	.257	.256	.269	.258	.255	.252	.207	.268
HW	.184	.196	.191	.194	.196	.190	.191	.194	.195	.207	.199
C1L	.200	.216	.212	.214	.198	.208	.204	.195	.200	.217	.227
C1A	.201	.216	.216	.222	.217	.218	.217	.233	.233	.188	.246
C1P	.051	.068	.068	.063	.070	.066	.066	.068	.061	.066	.065
C3L	.225	.225	.216	.230	.230	.230	.240	.227	.222	.217	.222
C3W	.211	.216	.225	.224	.226	.218	.233	.233	.218	.198	.238
C5L	.184	.180	.178	.174	.178	.174	.174	.194	.180	.179	.173
C5W	.244	.216	.217	.206	.220	.222	.212	.228	.220	.226	.218
DKL	.200	.851	.866	.878	.794	.571	.944	.900	1.166	1.000	1.000
DKC	.266	1.148	1.266	1.030	1.058	1.000	1.277	1.500	1.666	1.000	1.000
SIM	.000	.555	.400	.454	.235	.142	.277	.300	.000	.000	.083
AXL	.106	.138	.153	.142	.146	.140	.152	.142	.148	.160	.150
INL	.222	.271	.265	.278	.285	.263	.271	.260	.267	.235	.284
NOT	.013	.007	.015	.013	.014	.027	.024	.013	.019	.028	.018
HPW	.372	.389	.387	.387	.381	.399	.389	.403	.389	.377	.406
FAW	.328	.341	.341	.325	.322	.332	.323	.334	.327	.330	.344
GUW	.186	.179	.178	.172	.172	.185	.171	.180	.178	.198	.184
AIC	.000	1.259	1.466	1.000	1.352	1.142	1.444	1.000	1.000	2.000	.666
M2C	.200	1.555	1.133	1.666	1.558	1.428	1.777	1.700	2.000	.000	2.000
M11	2.000	1.740	1.733	1.121	1.323	2.000	1.833	1.800	2.000	2.000	1.750

Table 20 (continued)

Character	Population 9B	10	11A	12	13
CWN	6.400	6.674	6.444	6.125	6.875
CWA	.649	.645	.654	.657	.635
CWP	.679	.660	.671	.665	.657
ABL	.288	.284	.266	.276	.268
AHW	.512	.479	.520	.518	.497
PHW	.458	.431	.447	.459	.437
TFW	.481	.459	.473	.479	.465
GUL	.170	.159	.171	.152	.158
HUL	.122	.108	.125	.126	.125
PEL	.041	.046	.057	.046	.043
FEL	.083	.079	.072	.057	.064
ANL	.244	.243	.264	.254	.254
SHT	.412	.388	.403	.413	.385
BRL	.264	.259	.269	.255	.259
HW	.201	.199	.197	.204	.194
C1L	.206	.207	.212	.201	.208
C1A	.229	.216	.229	.235	.232
C1P	.068	.059	.057	.077	.066
C3L	.228	.227	.229	.237	.224
C3W	.237	.224	.238	.231	.226
C5L	.179	.186	.178	.168	.180
C5W	.221	.221	.217	.216	.211
DKL	1.300	.883	1.444	.500	.937
DKC	1.600	1.139	1.444	.500	1.281
SIM	.600	.139	.000	.125	.031
AXL	.151	.159	.173	.170	.145
INL	.291	.265	.266	.277	.274
NOT	.016	.021	.022	.023	.020
HPW	.401	.379	.412	.414	.390
FAW	.335	.337	.334	.337	.329
GUW	.183	.184	.181	.178	.181
AIC	1.300	1.651	.888	1.500	.812
M2C	1.600	1.046	1.333	1.750	1.875
MII	2.000	1.930	2.000	1.750	1.968

14	15	16	17	18	19
6.962	6.900	6.935	6.666	7.541	7.133
.626	.625	.613	.638	.624	.638
.657	.658	.647	.656	.665	.671
.293	.286	.285	.282	.277	.273
.470	.487	.457	.503	.489	.506
.425	.437	.407	.450	.444	.458
.451	.468	.427	.486	.470	.481
.161	.153	.154	.158	.165	.171
.112	.126	.116	.117	.118	.106
.048	.032	.041	.044	.046	.049
.075	.062	.100	.070	.074	.067
.244	.269	.225	.272	.248	.257
.363	.378	.403	.385	.386	.413
.269	.266	.250	.266	.253	.264
.201	.195	.192	.194	.209	.199
.206	.209	.198	.200	.199	.198
.233	.221	.220	.223	.223	.231
.049	.050	.056	.062	.069	.072
.222	.224	.226	.230	.219	.229
.209	.213	.198	.222	.219	.228
.186	.185	.181	.189	.175	.176
.213	.214	.217	.203	.218	.219
1.074	1.500	1.548	1.333	.833	.733
1.407	1.700	1.774	1.666	1.083	1.133
.111	.100	.129	1.000	.166	.133
.169	.143	.171	.142	.142	.157
.269	.269	.265	.278	.265	.268
.017	.017	.019	.018	.022	.020
.375	.377	.370	.383	.391	.397
.335	.336	.303	.363	.334	.339
.175	.172	.170	.176	.183	.183
1.592	1.400	1.870	2.000	.458	.733
1.888	1.800	1.354	1.666	1.625	1.866
2.000	1.700	1.806	2.000	1.666	1.733

Table 20 (continued)

Character	Population 20A	20B
CWN	6.500	7.000
CWA	.670	.637
CWP	.688	.663
ABL	.273	.251
AHW	.507	.429
PHW	.475	.381
TFW	.488	.400
GUL	.133	.168
HUL	.139	.078
PEL	.053	.048
FEL	.079	.104
ANL	.229	.206
SHT	.445	.363
BRL	.251	.236
HW	.202	.198
C1L	.203	.199
C1A	.239	.213
C1P	.066	.066
C3L	.215	.221
C3W	.216	.206
C5L	.185	.179
C5W	.247	.218
DKL	.500	3.333
DKC	.500	3.666
SIM	1.000	.000
AXL	.176	.149
INL	.268	.254
NOT	.039	.017
HPW	.397	.361
FAW	.308	.296
GUW	.180	.197
AIC	2.000	2.000
M2C	2.000	1.333
M11	2.000	2.000

Overall Means
6.764
.633
.656
.279
.488
.434
.461
.159
.118
.047
.076
.249
.391
.259
.196
.206
.223
.063
.226
.221
.180
.217
.964
1.227
.220
.150
.269
.018
.386
.330
.178
1.210
1.526
1.751

Table 21. Standard deviations of each character for

	Population				
	1A	1B	2	3	4
Character					
CWN	.954	.912	.693	1.128	.875
CWA	.021	.022	.099	.048	.024
CWP	.019	.028	.099	.055	.029
ABL	.014	.014	.042	.022	.015
AHW	.020	.017	.073	.046	.019
PHW	.014	.012	.062	.036	.017
TFW	.013	.009	.067	.037	.016
GUL	.016	.012	.019	.019	.011
HUL	.017	.028	.029	.022	.016
PEL	.015	.016	.021	.014	.015
FEL	.019	.011	.026	.034	.016
ANL	.020	.011	.042	.044	.013
SHT	.012	.015	.063	.034	.013
BRL	.022	.018	.040	.022	.015
HW	.009	.009	.032	.017	.010
C1L	.012	.016	.033	.024	.011
C1A	.028	.016	.040	.025	.016
C1P	.009	.007	.014	.015	.011
C3L	.008	.008	.041	.020	.008
C3W	.021	.015	.030	.020	.012
C5L	.012	.013	.035	.023	.012
C5W	.021	.022	.039	.029	.016
DKL	.438	.480	.452	.545	.454
DKC	.480	.640	.560	.522	.491
SIM	.000	.650	.752	.652	.635
AXL	.022	.016	.026	.019	.015
INL	.025	.012	.041	.031	.018
NOT	.011	.013	.019	.016	.012
HPW	.016	.013	.053	.044	.026
FAW	.016	.018	.060	.025	.020
GUW	.016	.010	.031	.021	.010
AIC	.000	.926	.891	.819	.783
M2C	.630	.776	.702	.516	.768
MI1	.000	.277	.271	.331	.621

each population of Kinosternon integrum males.

5	6	7	8A	8B	9A
.957	.826	.769	.788	1.414	.970
.001	.016	.023	.025	.004	.031
.014	.028	.028	.036	.016	.033
.021	.015	.014	.011	.016	.014
.008	.016	.021	.026	.028	.023
.007	.019	.014	.026	.030	.021
.019	.017	.022	.026	.034	.017
.010	.013	.015	.015	.006	.011
.026	.017	.023	.030	.007	.021
.020	.014	.012	.013	.010	.016
.015	.015	.016	.015	.011	.017
.008	.024	.022	.020	.002	.015
.020	.018	.027	.019	.007	.017
.012	.019	.020	.013	.005	.015
.007	.011	.011	.008	.007	.007
.005	.019	.021	.015	.000	.020
.013	.022	.022	.017	.053	.019
.011	.011	.011	.012	.021	.008
.003	.014	.012	.011	.005	.009
.019	.017	.014	.020	.008	.018
.010	.013	.016	.012	.014	.015
.015	.013	.019	.013	.001	.015
.000	.514	.531	.421	.707	.594
.000	.696	.589	.910	.707	.618
.500	.685	.508	.000	.000	.427
.033	.023	.012	.010	.001	.026
.038	.015	.014	.015	.004	.019
.010	.023	.011	.010	.003	.013
.016	.036	.016	.026	.025	.015
.018	.036	.015	.024	.000	.017
.005	.007	.012	.014	.005	.025
1.154	.831	.946	.849	.000	.998
.816	.528	.550	.699	1.414	.460
.000	.528	.000	.000	.000	.000

Table 21 (continued)

Character	Population 9B	10	11A	11B	12
CWN	1.164	.731	1.214	.849	1.166
CWA	.013	.025	.026	.017	.030
CWP	.013	.032	.032	.015	.025
ABL	.015	.012	.012	.009	.006
AHW	.014	.027	.020	.019	.021
PHW	.011	.029	.028	.012	.022
TFW	.019	.026	.020	.015	.019
GUL	.012	.018	.012	.014	.012
HUL	.028	.022	.025	.021	.011
PEL	.021	.016	.022	.015	.024
FEL	.014	.015	.011	.018	.009
ANL	.031	.026	.019	.015	.018
SHT	.031	.022	.019	.014	.024
BRL	.015	.016	.012	.007	.007
HW	.073	.009	.011	.007	.007
C1L	.012	.017	.008	.013	.016
C1A	.033	.021	.025	.029	.023
C1P	.012	.010	.011	.006	.011
C3L	.014	.011	.020	.009	.011
C3W	.027	.012	.024	.027	.017
C5L	.071	.040	.016	.012	.015
C5W	.080	.045	.018	.015	.020
DKL	.744	.356	.487	.316	.527
DKC	.916	.645	.690	.516	.726
SIM	.707	.448	.000	.421	.707
AXL	.026	.015	.015	.013	.016
INL	.019	.019	.019	.011	.016
NOT	.010	.014	.010	.006	.017
HPW	.009	.018	.018	.013	.016
FAW	.024	.023	.009	.021	.022
GUW	.006	.012	.011	.012	.008
AIC	.886	.658	.755	.843	1.054
M2C	.925	.854	.786	.316	.707
MI1	.462	.377	.000	.000	.707

13	14	15	16	17	18
.650	.662	.725	1.855	.823	1.286
.021	.025	.022	.825	.020	.031
.029	.026	.023	.030	.016	.040
.017	.013	.011	.012	.014	.009
.015	.045	.015	.027	.023	.021
.021	.021	.012	.023	.017	.024
.020	.020	.015	.024	.021	.015
.015	.012	.014	.015	.017	.024
.021	.043	.014	.013	.023	.022
.019	.014	.009	.029	.015	.010
.018	.018	.010	.016	.019	.016
.027	.019	.009	.016	.030	.025
.027	.021	.010	.013	.016	.016
.018	.020	.010	.010	.017	.011
.010	.013	.006	.010	.008	.010
.016	.010	.011	.011	.012	.012
.018	.018	.012	.021	.012	.017
.007	.009	.011	.010	.011	.027
.011	.012	.011	.013	.014	.008
.013	.016	.015	.015	.021	.020
.010	.016	.019	.020	.011	.011
.011	.020	.017	.014	.019	.014
.438	.572	.650	.857	.875	.000
.438	.549	.869	.725	1.074	.966
.277	.423	.751	.235	.000	.316
.018	.014	.013	.015	.020	.020
.014	.019	.015	.020	.016	.020
.018	.012	.008	.013	.018	.013
.013	.020	.021	.024	.022	.018
.017	.019	.020	.028	.021	.018
.042	.019	.009	.013	.018	.020
.947	.797	.960	.777	.875	.994
.375	.751	.630	.704	.674	.699
.554	.000	.000	.323	.316	.000

Table 21 (continued)

Character	Population 19
CWN	.389
CWA	.023
CWP	.024
ABL	.006
AHW	.013
PHW	.013
TFW	.016
GUL	.012
HUL	.023
PEL	.021
FEL	.013
AHL	.024
SHT	.009
BRL	.008
HW	.005
C1L	.012
C1A	.012
C1P	.015
C3L	.012
C3W	.008
C5L	.024
C5W	.018
DKL	.651
DKC	.668
SIM	.000
AXL	.014
INL	.020
NOT	.011
HPW	.012
FAW	.018
GUW	.009
AIC	.000
M2C	.651
M11	.000

20A	20B
.707	.577
.002	.013
.018	.018
.029	.012
.047	.009
.007	.008
.000	.002
.005	.020
.013	.008
.020	.010
.009	.019
.000	.011
.006	.019
.005	.004
.020	.002
.005	.012
.006	.018
.005	.011
.008	.010
.008	.004
.000	.006
.027	.024
.000	.577
.707	.577
.000	.000
.021	.011
.018	.009
.008	.003
.014	.016
.011	.008
.005	.008
.000	.000
1.414	.000
.000	.000

Table 22. Standard deviations of each character for each population of *Kinosternon integrum* females.

Character	Population 1A	1B	2	3	4	5	6	7	8A	8B	9A
CWN	.414	.868	.457	.755	.618	.951	.704	.737	.408	.000	.389
CWA	.020	.020	.032	.023	.027	.022	.018	.017	.023	.000	.014
CWP	.026	.025	.036	.026	.033	.022	.022	.024	.025	.000	.024
ABL	.017	.014	.028	.012	.017	.015	.013	.012	.029	.000	.016
AHW	.013	.018	.028	.015	.027	.034	.017	.018	.020	.000	.014
PHW	.024	.010	.030	.020	.020	.014	.022	.019	.012	.000	.015
TFW	.018	.015	.033	.016	.020	.013	.020	.020	.017	.000	.017
GUL	.015	.010	.016	.011	.013	.024	.016	.016	.012	.000	.014
HUL	.015	.032	.019	.020	.021	.033	.022	.022	.022	.000	.024
PEL	.008	.020	.017	.018	.020	.012	.017	.013	.019	.000	.013
FEL	.015	.011	.017	.016	.019	.011	.017	.016	.028	.000	.014
ANL	.020	.014	.020	.015	.020	.011	.017	.019	.028	.000	.018
SHT	.024	.017	.032	.019	.018	.023	.025	.020	.028	.000	.028
BRL	.011	.016	.034	.011	.021	.016	.018	.009	.026	.000	.008
HW	.004	.006	.010	.007	.006	.006	.009	.007	.006	.000	.010
C1L	.009	.014	.020	.012	.013	.014	.013	.025	.019	.000	.013
C1A	.026	.014	.025	.014	.018	.027	.015	.035	.019	.000	.016
C1P	.009	.007	.011	.011	.009	.014	.010	.008	.012	.000	.009
C3L	.009	.011	.024	.014	.018	.013	.020	.009	.006	.000	.016
C3W	.015	.015	.012	.013	.021	.009	.015	.024	.011	.000	.012
C5L	.011	.011	.012	.010	.016	.017	.017	.019	.007	.000	.014
C5W	.017	.018	.020	.018	.022	.033	.019	.020	.013	.000	.018
DKL	.414	.533	.351	.415	.478	.534	.639	.567	.408	.000	.426
DKC	.593	.662	.457	.394	.488	.577	.751	.849	1.211	.000	.426
SIM	.000	.751	.507	.711	.495	.377	.574	.674	.000	.000	.288
AXL	.018	.020	.019	.014	.011	.026	.020	.016	.035	.000	.020
INL	.030	.041	.023	.017	.019	.016	.017	.021	.029	.000	.022
NOT	.007	.038	.005	.007	.009	.027	.010	.007	.012	.000	.011
HPW	.017	.025	.026	.011	.021	.014	.018	.019	.026	.000	.031
FAW	.023	.018	.024	.022	.017	.008	.018	.018	.013	.000	.013
GUW	.015	.010	.014	.011	.014	.025	.014	.012	.012	.000	.011
AIC	.000	.902	.915	.866	.848	1.069	.855	1.054	1.095	.000	.887
M2C	.560	.751	.833	.595	.746	.975	.548	.674	.000	.000	.000
M11	.000	.594	.457	.484	.806	.000	.514	.421	.000	.000	.621

Table 22 (continued)

	Population				
	9B	10	11A	12	13
Character					
CWN	.516	.644	.726	.353	.870
CWA	.014	.025	.021	.026	.026
CWP	.020	.028	.016	.022	.030
ABL	.016	.015	.010	.014	.017
AHW	.016	.029	.028	.024	.024
PHW	.010	.028	.015	.027	.024
TFW	.015	.029	.014	.027	.025
GUL	.013	.015	.029	.009	.023
HUL	.024	.020	.026	.015	.026
PEL	.008	.017	.019	.020	.016
FEL	.022	.018	.020	.014	.017
ANL	.021	.023	.019	.025	.022
SHT	.022	.031	.016	.023	.020
BRL	.016	.018	.013	.011	.025
HW	.013	.008	.006	.007	.014
C1L	.014	.014	.015	.006	.016
C1A	.023	.020	.011	.026	.021
C1P	.013	.010	.015	.007	.010
C3L	.005	.012	.010	.012	.016
C3W	.013	.017	.012	.010	.016
C5L	.014	.013	.005	.012	.014
C5W	.015	.019	.013	.011	.017
DKL	.674	.447	.726	.755	.564
DKC	.843	.742	.726	.755	.522
SIM	.966	.412	.000	.353	.176
AXL	.012	.020	.023	.020	.019
INL	.031	.026	.012	.019	.016
NOT	.008	.014	.029	.010	.016
HPW	.010	.021	.022	.011	.017
FAW	.014	.020	.015	.012	.020
GUW	.007	.016	.011	.011	.017
AIC	.823	.752	.927	.925	.965
M2C	.516	.924	.866	.707	.491
MII	.000	.337	.000	.462	.176

4	15	16	17	18	19
517	.316	.727	.577	.658	.743
025	.018	.020	.035	.019	.020
023	.024	.022	.023	.018	.015
018	.013	.018	.020	.014	.015
039	.013	.024	.024	.024	.018
038	.013	.024	.022	.020	.018
054	.021	.024	.020	.023	.018
012	.016	.022	.018	.016	.012
019	.011	.021	.020	.015	.024
014	.011	.016	.028	.017	.018
017	.022	.019	.014	.013	.018
022	.030	.018	.028	.018	.020
033	.017	.026	.043	.027	.017
015	.014	.018	.003	.016	.010
008	.009	.009	.001	.049	.005
010	.014	.016	.021	.011	.012
026	.014	.017	.045	.016	.017
007	.010	.011	.006	.011	.010
010	.012	.013	.002	.017	.009
015	.017	.016	.007	.015	.014
023	.010	.015	.007	.010	.010
019	.022	.020	.010	.021	.015
729	.707	.722	.577	.481	.457
843	.823	.668	.577	.583	.833
423	.316	.427	1.000	.481	.516
017	.055	.017	.004	.039	.023
016	.012	.021	.017	.020	.029
011	.006	.015	.015	.027	.008
018	.019	.021	.020	.020	.019
020	.026	.019	.023	.019	.023
014	.016	.012	.024	.015	.020
797	.966	.499	.000	.658	.883
423	.421	.754	.577	.575	.516
000	.674	.401	.000	.637	.593

Table 22 (continued)

	Population	
	20A	20B
Character		
CWN	.707	1.000
CWA	.029	.040
CWP	.030	.050
ABL	.002	.018
AHW	.009	.018
PHW	.001	.016
TFW	.004	.014
GUL	.023	.013
HUL	.026	.006
PEL	.016	.014
FEL	.006	.006
ANL	.018	.013
SHT	.017	.005
BRL	.014	.004
HW	.003	.016
C1L	.016	.008
C1A	.031	.006
C1P	.000	.017
C3L	.001	.015
C3W	.011	.012
C5L	.002	.008
C5W	.007	.015
DKL	.707	.577
DKC	.707	.577
SIM	1.414	.000
AXL	.001	.012
INL	.003	.015
NOT	.015	.002
HPW	.019	.009
FAW	.000	.012
GUW	.008	.004
AIC	.000	.000
M2C	.000	1.154
M11	.000	.000

Overall
Means

Table 23. Within populations correlation coefficients for Kinosternon integrum males (* = significant at .05 level, ** = significant at .01 level).

Character	CWN	CWA	CWP	ABL	AHW	PHW	TFW	GUL	HUL	PEL	FEL
CWN	1.000										
CWA	-.064	1.000									
CWP	.145	.904 **	1.000								
ABL	.051	.473 *	.426 *	1.000							
AHW	-.012	.738 **	.681 **	.454 *	1.000						
PHW	.061	.799 **	.838 **	.476 *	.755 **	1.000					
TFW	.106	.725 **	.750 **	.569 **	.779 **	.879 **	1.000				
GUL	-.076	.292	.245	.305	.370	.279	.334	1.000			
HUL	.010	.360	.354	.090	.351	.365	.347	-.157	1.000		
PEL	.064	.174	.192	.172	.100	.187	.173	.023	-.391	1.000	
FEL	-.010	.314	.311	.093	.205	.191	.139	.096	.084	.113	1.000
ANL	.061	.444 *	.442 *	.305	.458 *	.536 **	.537**	.244	.224	.087	-.389
SHT	.070	.659 **	.651 **	.546 **	.638 **	.658 **	.649**	.260	.265	.149	.241
BRL	-.032	.534 **	.460 *	.667 **	.648 **	.573 **	.610**	.290	.170	.117	.087
HW	.033	.469 *	.418 *	.412 *	.374	.406 *	.459*	.220	.136	.070	.102
C1L	.012	.652 **	.657 **	.224	.553 **	.546 **	.476*	.250	.340	.023	.282
C1A	-.004	.575 **	.558 **	.325	.477 *	.554 **	.478*	.219	.234	.109	.179
C1P	-.019	.331	.280	.218	.188	.302	.246	.117	.047	.174	.122
C3L	-.042	.631 **	.565 **	.563 **	.564 **	.558 **	.595**	.226	.266	.123	.199
C3W	-.045	.551 **	.517 **	.280	.417 *	.486 *	.451*	.138	.258	.124	.119
C5L	.053	.284	.259	.408 *	.275	.204	.267	.258	.041	.164	.068
C5W	.046	.392	.387	.354	.372	.322	.326	.221	.133	.135	.127
DKL	.021	.051	.075	.033	.051	.027	-.010	-.026	-.050	.112	.095
DKC	.081	.057	.112	-.088	.032	.017	-.013	-.081	.028	.055	.048
SIM	-.011	-.068	-.121	.069	-.012	-.020	-.016	-.008	.001	-.053	-.118
AXL	.030	.393	.377	.298	.316	.295	.267	.212	.106	.092	.126
INL	-.049	.623 **	.612 **	.426 *	.509 **	.555 **	.506 **	.295	.258	.053	.191
NOT	.007	-.133	-.165	.001	-.095	-.189	-.091	-.002	-.077	-.062	-.043
HPW	-.019	.641 **	.606 **	.449 *	.697 **	.616 **	.651 **	.386	.245	.129	.193
FAW	.101	.550 **	.541 **	.516 **	.537 **	.598 **	.675 **	.200	.216	.112	.126
GUW	-.024	.504 *	.485 *	.323	.450	.440 *	.411 *	.376	.131	.089	.167
AIC	-.000	.030	.004	.030	-.109	-.071	-.102	-.043	-.012	.020	.024
M2C	.014	.014	-.002	.087	.080	.085	.091	-.040	.045	.074	-.032
MII	.012	-.053	-.085	.046	-.034	-.055	-.020	-.025	-.033	-.003	-.053

Table 23 (continued)

Character	ANL	SHT	BRL	HW	C1L
ANL	1.000				
SHT	.305	1.000			
BRL	.361	.481*	1.000		
HW	.160	.482*	.343	1.000	
C1L	.325	.487*	.274	.316	1.000
C1A	.300	.474*	.368	.300	.576**
C1P	.096	.302	.182	.305	.122
C3L	.300	.636**	.513 **	.472 *	.446 *
C3W	.241	.504*	.329	.361	.347
C5L	.058	.201	.343	.295	.089
C5W	.104	.242	.367	.234	.157
DKL	.054	.105	-.070	-.100	.131
DKC	.072	.055	-.105	-.145	.200
SIM	.047	-.012	.022	.015	-.082
AXL	.165	.372	.241	.256	.239
INL	.347	.475*	.492 *	.250	.460 *
NOT	-.519 **	.038	.000	.184	-.140
HPW	.346	.552**	.483 *	.354	.500 *
FAW	.292	.511**	.481 *	.441 *	.305
GUW	.316	.361	.330	.227	.368
AIC	-.079	.019	-.104	.080	.019
M2C	.016	.035	.104	.061	.057
M11	-.134	.010	.085	.005	-.090

C1A	C1P	C3L	C3W	C5L	C5W
1.000					
.304	1.000				
.464 *	.215	1.000			
.462 *	.370	.492 *	1.000		
.104	.006	.289	.200	1.000	
.163	.145	.266	.300	.774 **	1.000
.032	-.165	.087	-.117	-.063	-.070
.008	-.215	.030	-.061	-.097	-.118
-.049	.040	-.029	-.075	-.104	-.119
.227	.092	.282	.197	.118	.211
.460 *	.129	.416 *	.369	.250	.322
-.096	-.012	.028	-.022	.169	.079
.397	.177	.529 **	.387	.290	.338
.354	.283	.453 *	.375	.337	.339
.312	.237	.357	.264	.125	.186
.005	.066	.004	.006	.093	.117
.377	.094	.041	.068	-.030	-.048
-.153	-.034	.024	-.000	.053	.004

Table 23 (continued)

	Character				
	DKL	DKC	SIM	AXL	INL
Character					
DKL	1.000				
DKC	.643**	1.000			
SIM	.025	-.018	1.000		
AXL	.167	.106	-.031	1.000	
INL	.066	.036	-.107	.347	1.000
NOT	-.120	-.148	.056	-.029	-.151
HPW	.046	.036	-.056	.325	.519 **
FAW	-.023	-.058	-.045	.225	.390
GUW	-.018	.018	-.032	.263	.342
AIC	.013	-.006	.119	.325	.094
M2C	-.005	-.091	.051	.065	.120
M11	-.048	-.035	.076	.091	-.025

	M11
M11	1.000

NOT	HPW	FAW	GUW	AIC	M2C
1.000					
-.012	1.000				
.038	.590**	1.000			
-.121	.428*	.333	1.000		
-.028	-.059	-.066	.004	1.000	
.029	.007	.090	-.037	-.032	1.000
.216	.144	.116	-.149	-.006	.080

Table 24. Within populations correlation coefficients for <u>Kinosternon</u> <u>integrum</u> females (* = significant at .05 level, ** = significant at .01 level).

Character	CWN	CWA	CWP	ABL	AHW	PHW	TFW	GUL	HUL	PEL	FEL
CWN	1.000										
CWA	-.095	1.000									
CWP	.202	.767 **	1.000								
ABL	-.074	.076	.032	1.000							
AHW	-.116	.501 *	.470 *	.164	1.000						
PHW	-.020	.491 *	.580 **	.203	.740 **	1.000					
TFW	-.050	.315	.396	.274	.744 **	.863 **	1.000				
GUL	-.058	.125	.079	-.017	.213	.180	.158	1.000			
HUL	.011	.128	.141	-.109	.191	.082	.076	-.352	1.000		
PEL	.024	.042	.075	.037	-.015	.121	.081	-.097	-.579 **	1.000	
FEL	-.034	.135	.121	-.132	-.096	-.078	-.146	-.057	.030	.082	1.000
ANL	-.049	.162	.139	.251	.450 *	.420 *	.430 *	.166	.079	-.061	-.603 **
SHT	-.059	.222	.206	.289	.361	.486 *	.445 *	.149	-.038	.121	-.035
BRL	-.100	.185	.171	.520 *	.407 *	.394	.435 *	-.001	-.021	.053	-.174
HW	.021	.158	.113	-.006	.061	.116	.071	.096	-.011	-.030	-.048
C1L	-.052	.259	.234	-.161	.184	.128	.063	.028	.225	-.012	.148
C1A	-.002	.310	.302	-.051	.230	.237	.136	.087	.102	.040	.081
C1P	-.034	.197	.176	.064	.151	.215	.121	.103	.011	.022	.006
C3L	-.008	.113	.095	.238	.185	.252	.240	.011	-.046	.070	.109
C3W	-.074	.282	.311	.112	.226	.340	.261	.063	.073	.103	.017
C5L	.080	.008	.007	-.016	-.042	-.004	.036	-.014	-.060	.066	-.109
C5W	.230	.041	.185	-.048	.030	.072	.082	-.028	.006	.062	-.044
DKL	.024	-.030	-.001	-.042	-.070	-.053	-.056	-.019	-.050	.029	-.016
DKC	.019	-.019	.029	-.122	-.010	-.062	-.054	.017	.003	.060	-.014
SIM	.034	-.018	.050	.049	.073	.040	.034	-.032	-.050	.059	-.012
AXL	.034	.118	.089	-.046	-.000	.010	.007	-.017	-.054	.115	.130
INL	-.076	.172	.199	.214	.253	.271	.194	.017	.064	.036	-.005
NOT	.076	-.060	-.052	-.060	-.100	-.070	-.067	-.026	-.109	.077	.007
HPW	-.040	.340	.332	.094	.609 **	.404 *	.413 *	.302	.053	.078	.017
FAW	.013	.292	.317	.066	.240	.336	.385	-.030	-.006	.158	-.031
GUW	-.034	.188	.133	-.061	.170	.094	.095	.280	-.022	.042	.088
AIC	-.023	.158	.100	-.038	.030	.033	-.023	-.066	.012	.064	.049
M2C	.074	-.150	-.068	-.076	-.077	-.066	-.065	-.036	-.032	.034	-.024
M1I	-.034	-.045	-.047	-.022	.005	.013	.037	-.004	-.093	.106	-.101

Table 24 (continued)

	Character				
	ANL	SHT	BRL	HW	C1L
Character					
ANL	1.000				
SHT	.296	1.000			
BRL	.405*	.405*	1.000		
HW	-.001	.102	-.083	1.000	
C1L	-.009	.041	-.122	.040	1.000
C1A	-.002	.115	.056	.048	.337
C1P	.024	.166	-.082	.129	.049
C3L	.000	.372	.326	.115	-.009
C3W	.118	.285	.179	.037	.025
C5L	.101	.017	-.097	.070	-.155
C5W	.073	-.025	-.052	.046	-.172
DKL	.088	.017	-.103	-.030	.091
DKC	.067	-.033	-.169	.003	.184
SIM	-.011	.076	.087	.043	-.019
AXL	-.038	.084	.044	-.021	.056
INL	.196	.192	.303	-.076	.097
NOT	-.313	-.085	-.162	.097	.047
HPW	.229	.146	.218	.035	.219
FAW	.105	.120	.147	.081	.054
GUW	.051	.022	-.097	.069	.172
AIC	-.016	.061	-.039	.033	.084
M2C	-.114	-.018	-.026	.061	.035
M11	.058	.045	.170	.039	-.027

C1A	C1P	C3L	C3W	C5L	C5W
1.000					
.175	1.000				
.087	.026	1.000			
.254	.220	.298	1.000		
-.201	-.091	-.226	-.066	1.000	
-.123	-.065	-.313	-.017	.426 *	1.000
.019	-.120	.001	-.066	.004	-.022
.084	-.070	-.056	-.068	.032	-.067
.020	.015	-.036	.064	-.070	-.001
.005	-.097	.048	.001	.029	-.022
.133	.123	.015	.156	-.085	-.052
-.054	-.021	-.036	-.156	.014	.035
.198	.092	.016	.075	-.103	.045
.153	.097	-.000	.152	.131	.157
.162	.112	-.044	-.036	-.043	-.005
.054	.040	-.108	.093	.040	.020
.283	.065	.099	.109	-.071	-.036
-.041	-.203	.037	-.075	.008	.034

Table 24 (continued)

Character	DKL	DKC	SIM	AXL	INL
DKL	1.000				
DKC	.632 **	1.000			
SIM	.002	.020	1.000		
AXL	.038	.111	-.065	1.000	
INL	.002	.003	.202	.009	1.000
NOT	-.051	-.021	.064	-.023	.137
HPW	-.019	.080	.065	.004	.298
FAW	-.063	-.034	.029	.060	.082
GUW	.016	.099	-.030	.002	-.086
AIC	-.056	-.014	.106	.408	.135
M2C	-.012	.044	.026	.008	-.039
M11	-.095	-.036	.004	.086	-.018

	M11
M11	1.000

NOT	HPW	FAW	GUW	AIC	M2C
1.000					
.157	1.000				
.148	.218	1.000			
-.036	.265	.012	1.000		
.058	.019	.075	-.036	1.000	
.048	-.092	-.013	-.033	-.029	1.000
.019	.061	.053	.091	.055	.024

Table 25. Number of specimens assigned to each population by multiple discriminant analysis of Kinosternon integrum males.

Number of Specimens Assigned to Population:

Original Population	1A	1B	2	3	4	5	6	7	8A	8B	9A	9B	10	11A	11B	12	13	14	15	16	17	18	19	20A	20B
1A	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1B	0	11	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	4	12	0	1	1	1	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	2	0
3	0	0	3	27	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
4	0	0	1	1	21	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
5	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	1	1	0	7	3	2	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0
7	0	0	0	0	0	1	2	10	0	0	3	0	2	2	1	1	0	0	0	0	0	1	1	0	0
8A	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
8B	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9A	0	0	1	0	0	0	0	1	0	0	9	0	0	3	1	0	1	0	0	0	2	0	0	0	0
9B	0	0	0	0	1	0	1	0	1	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	1	0	1	0	0	0	0	1	1	0	1	19	0	0	0	0	2	0	0	0	0	1	1	0
11A	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	1	0	0	0	0	0	0	0	0
11B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0

Table 25 (continued)

Number of Specimens Assigned to Population:

Original Population	1A 14	1B 15	2 16	3 17	4 18	5 19	6 20A	7 20B
12	0	0	0	0	0	0	0	0
	0	0	0	0	0	1	0	0
13	0	0	0	0	1	0	1	1
	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0
	21	4	1	0	0	0	0	0
15	0	0	0	0	0	0	0	0
	1	11	1	0	0	0	0	0
16	0	0	0	0	0	0	0	0
	0	1	15	1	0	0	1	0
17	0	0	0	0	0	0	0	0
	1	0	1	5	0	0	0	0
18	0	0	0	0	0	0	0	0
	0	0	0	0	8	0	0	0
19	0	0	0	0	0	0	1	0
	0	0	0	0	0	11	0	0
20A	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	2	0
20B	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	3

8A	8B	9A	9B	10	11A	11B	12	13
0	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	8
0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	1	2	0	0	0
1	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

Table 26. Number of specimens assigned to each population by multiple discriminant analysis of Kinosternon integrum females.

Number of Specimens Assigned to Population:

Original Population	1A	1B	2	3	4	5	6	7	8A	8B	9A	9B	10	11A	12	13	14	15	16	17	18	19	20A	20B
1A	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1B	0	20	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
2	0	1	11	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0
3	0	3	2	21	2	0	0	0	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0
4	0	0	1	2	23	1	2	0	0	0	0	0	0	1	0	2	1	1	0	0	0	0	0	0
5	0	0	0	0	1	4	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
6	0	0	0	0	1	0	14	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
7	0	1	1	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
8A	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8B	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9A	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0
9B	0	0	0	0	0	0	0	1	0	0	0	7	1	0	0	1	0	0	0	0	0	0	0	0
10	0	0	3	1	1	1	0	1	0	0	0	5	28	0	0	0	1	1	0	0	0	1	0	0
11A	0	0	0	0	0	0	0	0	1	0	1	0	0	7	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	1	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0

Table 26 (continued)

Number of Specimens Assigned to Population:

Original Population	1A	1B	2	3	4	5	6	7
	15	16	17	18	19	20A	20B	
13	0	0	2	0	0	0	0	1
	2	0	0	1	0	0	0	
14	0	0	0	0	0	0	0	0
	2	1	0	0	0	0	0	
15	0	0	0	0	0	0	0	0
	7	1	0	0	0	0	0	
16	0	0	0	0	2	0	1	0
	0	24	0	0	1	0	0	
17	0	1	0	0	0	0	0	0
	0	0	2	0	0	0	0	
18	0	0	0	2	1	1	0	0
	2	0	0	12	4	0	0	
19	0	1	0	0	0	0	0	0
	0	0	0	2	9	0	0	
20A	0	0	0	0	0	0	0	0
	0	0	0	0	0	2	0	
20B	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	3	

8A	8B	9A	9B	10	11A	12	13	14
2	1	1	2	1	0	0	18	1
0	0	0	0	2	0	0	0	22
0	0	0	1	0	0	0	0	1
1	0	0	0	1	1	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	1	0
0	0	0	0	0	0	2	1	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

Table 27. Summary table of multiple discriminant analysis of *Kinosternon integrum* males.

Step	Variable Selected	F Value
1	M1O	10.414
2	DKL	8.996
3	INL	5.753
4	BRL	7.562
5	AXL	6.241
6	AHW	5.097
7	CWA	4.422
8	PHW	4.881
9	GUL	3.798
10	C1A	3.602
11	C3L	3.877
12	C1L	3.198
13	TFW	3.047
14	PEL	2.859
15	CWP	2.856
16	HPW	2.417
17	M2C	2.342
18	AIC	2.301
19	HW	2.301
20	C3W	2.344
21	C1P	2.083
22	DKC	1.891
23	GUW	1.920
24	ABL	1.809
25	SHT	1.923
26	FEL	1.553
27	FAW	1.529
28	HUL	1.423
29	C5W	1.495
30	NOT	1.556
31	ANL	2.138
32	CWN	1.237
33	SIM	1.048
34	C5L	.959

Table 28. Summary table of multiple discriminant analysis of _Kinosternon_ _integrum_ females.

Step	Variable Entered	F Value
1	AHW	8.234
2	ABL	7.265
3	AXL	6.497
4	DKL	5.568
5	SHT	5.542
6	M1O	5.363
7	M2C	4.927
8	INL	4.455
9	ANL	4.414
10	C3W	4.155
11	C1L	3.981
12	BRL	4.131
13	PHW	3.365
14	HUL	3.247
15	PEL	3.570
16	FEL	3.134
17	AIC	2.988
18	GUL	2.695
19	CWN	2.642
20	C3L	2.643
21	C1P	2.475
22	HPW	2.333
23	FAW	2.197
24	C5W	1.977
25	C1A	1.713
26	SIM	1.626
27	DKC	1.609
28	GUW	1.532
29	HW	1.476
30	CWA	1.337
31	CWP	1.856
32	TFW	1.384
33	NOT	1.328
34	C5L	1.221

Table 29. Mean value of each character for each population of Kinosternon scorpioides males, expressed as a proportion of CL except as described in the text.

Character	Population 21	22	23	24	25	26	27	28	29	30	31
CWN	6.333	6.083	5.818	7.875	6.666	6.333	6.200	6.243	5.833	6.000	6.200
CWA	.651	.657	.650	.614	.627	.612	.632	.617	.619	.631	.600
CWP	.650	.656	.651	.645	.635	.615	.644	.620	.612	.631	.601
ABL	.263	.248	.226	.310	.253	.258	.276	.259	.266	.276	.263
AHW	.505	.502	.509	.491	.485	.483	.503	.483	.482	.492	.488
PHW	.443	.439	.425	.418	.432	.440	.437	.406	.389	.421	.424
TFW	.487	.478	.480	.474	.471	.480	.477	.457	.445	.466	.462
GUL	.154	.148	.160	.172	.151	.169	.149	.156	.167	.183	.157
HUL	.138	.151	.143	.111	.130	.144	.150	.125	.128	.121	.141
PEL	.027	.024	.024	.027	.028	.030	.026	.027	.014	.007	.028
FEL	.049	.056	.077	.025	.056	.042	.048	.046	.046	.054	.057
ANL	.308	.285	.293	.300	.293	.332	.317	.311	.313	.299	.313
SHT	.457	.430	.439	.375	.403	.442	.424	.400	.394	.421	.443
BRL	.301	.298	.271	.284	.291	.277	.297	.292	.288	.299	.280
HW	.205	.197	.205	.189	.195	.215	.209	.191	.190	.192	.223
C1L	.219	.221	.238	.213	.226	.221	.219	.217	.211	.200	.225
C1A	.206	.224	.231	.213	.223	.215	.215	.241	.230	.230	.232
C1P	.056	.057	.059	.060	.058	.073	.063	.068	.061	.073	.062
C3L	.224	.236	.220	.213	.222	.230	.225	.218	.215	.221	.224
C3W	.178	.161	.194	.184	.192	.184	.184	.176	.168	.166	.173
C5L	.194	.191	.194	.185	.191	.200	.204	.197	.192	.199	.201
C5W	.211	.214	.229	.223	.215	.215	.231	.228	.214	.226	.230
DKL	3.500	2.708	1.636	3.125	2.000	2.666	3.800	2.243	3.666	3.000	3.200
DKC	3.500	2.708	1.636	3.125	2.333	2.666	3.800	1.918	2.916	2.750	2.800
SIM	.166	.000	.000	.000	.166	.333	.400	.108	.083	.000	.000
AXL	.159	.161	.113	.000	.162	.163	.167	.161	.167	.143	.223
INL	.270	.262	.222	.248	.263	.237	.267	.266	.266	.259	.242
NOT	.002	.000	.000	.005	.000	.000	.001	.000	.000	.000	.000
HPW	.379	.383	.354	.377	.383	.384	.370	.366	.375	.380	.371
FAW	.352	.355	.394	.349	.361	.369	.353	.349	.329	.345	.315
GUW	.168	.155	.157	.176	.167	.166	.165	.167	.162	.171	.173
AIC	.166	.083	.181	.000	.333	.000	.000	.216	.083	.000	.000
M2C	.333	1.166	1.818	.375	1.333	1.333	.600	2.000	1.916	1.250	1.500
M11	1.666	1.791	1.727	2.000	2.000	1.666	1.600	1.702	1.583	1.000	1.300

Table 29 (continued)

Character	Population 32	33	34	35	36
CWN	6.200	6.000	6.361	5.628	6.588
CWA	.668	.629	.623	.625	.641
CWP	.680	.637	.631	.621	.653
ABL	.228	.229	.256	.283	.277
AHW	.515	.493	.493	.501	.508
PHW	.466	.428	.435	.426	.437
TFW	.500	.482	.481	.475	.497
GUL	.168	.162	.154	.163	.156
HUL	.146	.145	.142	.144	.154
PEL	.023	.027	.034	.020	.016
FEL	.057	.059	.043	.031	.029
ANL	.312	.294	.286	.298	.299
SHT	.420	.413	.406	.413	.420
BRL	.247	.239	.237	.253	.254
HW	.207	.198	.204	.206	.209
C1L	.226	.222	.218	.230	.221
C1A	.217	.224	.202	.216	.205
C1P	.063	.047	.062	.054	.053
C3L	.223	.223	.220	.225	.230
C3W	.206	.190	.193	.188	.174
C5L	.218	.197	.201	.206	.203
C5W	.243	.221	.224	.217	.230
DKL	4.000	3.000	2.583	2.714	2.470
DKC	1.400	3.000	2.222	2.342	2.058
SIM	.000	.200	.166	.071	.176
AXL	.116	.130	.196	.211	.181
INL	.254	.303	.274	.288	.270
NOT	.000	.000	.002	.000	.000
HPW	.398	.324	.383	.388	.398
FAW	.307	.395	.383	.372	.391
GUW	.184	.181	.172	.167	.167
AIC	1.200	1.600	1.861	1.785	2.000
M2C	.800	2.000	.611	1.085	.529
M11	1.400	1.800	1.472	.985	2.000

37	38	39	40	42	43
6.172	6.500	6.500	.058	5.738	6.000
.638	.617	.601	.216	.615	.596
.637	.619	.614	.180	.609	.595
.278	.264	.247	.199	.289	.279
.493	.472	.453	.210	.497	.478
.418	.396	.370	2.888	.423	.409
.473	.439	.414	2.777	.458	.453
.158	.151	.157	.000	.169	.165
.130	.132	.123	.175	.151	.131
.031	.028	.029	.255	.014	.026
.042	.046	.048	.015	.026	.037
.284	.278	.257	.364	.301	.294
.407	.390	.399	.320	.428	.416
.251	.241	.225	.181	.263	.245
.208	.205	.235	1.888	.209	.205
.218	.208	.204	.722	.244	.233
.196	.209	.205	1.833	.221	.217
.059	.069	.071	6.722	.047	.063
.222	.224	.228	.606	.220	.225
.172	.173	.173	.621	.184	.178
.191	.194	.191	.265	.205	.203
.211	.200	.200	.444	.206	.214
2.896	2.777	3.250	.366	2.880	2.687
2.379	1.611	2.250	.401	2.404	2.250
.068	.055	1.000	.169	.357	.312
.192	.223	.175	.091	.225	.229
.261	.262	.264	.033	.274	.284
.000	.002	.018	.070	.000	.000
.386	.355	.382	.243	.379	.372
.362	.377	.353	.362	.339	.349
.175	.171	.187	.243	.169	.165
1.724	2.000	2.000	.210	1.476	1.562
.551	.666	.500	.206	1.190	1.375
1.586	1.888	2.000	.204	1.238	.937

Table 29 (continued)

Character	Population 44	45	46	47	48
CWN	6.600	6.400	8.000	7.000	6.600
CWA	.648	.599	.559	.634	.608
CWP	.638	.601	.598	.660	.624
ABL	.277	.261	.220	.262	.261
AHW	.514	.424	.433	.460	.430
PHW	.436	.349	.346	.367	.364
TFW	.477	.380	.362	.404	.380
GUL	.145	.164	.149	.157	.136
HUL	.159	.083	.094	.125	.103
PEL	.014	.038	.039	.024	.032
FEL	.024	.075	.078	.086	.105
ANL	.290	.223	.220	.235	.193
SHT	.403	.352	.354	.341	.352
BRL	.277	.235	.212	.255	.246
HW	.206	.211	.212	.204	.206
C1L	.240	.202	.236	.208	.207
C1A	.216	.199	.220	.218	.231
C1P	.049	.061	.078	.063	.065
C3L	.232	.213	.220	.226	.218
C3W	.178	.187	.196	.212	.187
C5L	.200	.205	.189	.170	.183
C5W	.227	.210	.196	.217	.208
DKL	3.200	2.720	4.000	2.000	3.000
DKC	3.200	2.240	4.000	2.000	3.200
SIM	.400	.000	.000	.333	.400
AXL	.185	.156	.157	.152	.156
INL	.285	.281	.236	.230	.241
NOT	.008	.015	.031	.037	.034
HPW	.401	.366	.362	.365	.343
FAW	.357	.288	.307	.321	.297
GUW	.175	.172	.181	.162	.153
AIC	1.600	1.920	2.000	2.000	2.000
M2C	1.200	.320	.000	.000	1.600
MI1	2.000	1.920	2.000	2.000	2.000

49	50	51	52	53	54
6.000	7.125	6.666	8.000	6.000	8.000
.601	.596	.603	.604	.609	.589
.619	.631	.617	.623	.619	.642
.267	.254	.270	.250	.253	.264
.401	.430	.428	.437	.436	.463
.349	.349	.365	.357	.360	.364
.356	.369	.400	.379	.377	.410
.131	.135	.155	.148	.142	.165
.078	.101	.109	.102	.096	.099
.075	.048	.035	.022	.035	.019
.112	.093	.091	.080	.129	.053
.196	.204	.216	.215	.212	.251
.368	.347	.331	.338	.332	.370
.236	.239	.249	.244	.242	.271
.195	.189	.203	.219	.214	.185
.202	.216	.207	.196	.201	.205
.173	.212	.192	.205	.201	.211
.067	.061	.064	.074	.072	.086
.229	.219	.208	.202	.211	.218
.191	.189	.167	.193	.179	.158
.187	.185	.204	.189	.186	.211
.221	.209	.217	.214	.200	.218
3.500	3.500	3.333	3.500	4.000	4.000
3.500	3.625	3.333	4.000	4.000	4.000
.000	.000	.000	.000	.000	2.000
.161	.159	.160	.147	.145	.158
.240	.250	.241	.234	.242	.258
.041	.033	.035	.013	.005	.046
.330	.348	.354	.357	.346	.370
.308	.302	.320	.324	.301	.291
.142	.163	.162	.174	.162	.165
2.000	2.000	2.000	2.000	2.000	2.000
.000	.875	.666	.000	.000	2.000
2.000	1.875	1.333	1.000	2.000	.000

Table 29 (continued)

Character	Overall Means
CWN	6.194
CWA	.622
CWP	.625
ABL	.268
AHW	.484
PHW	.412
TFW	.456
GUL	.159
HUL	.132
PEL	.026
FEL	.047
ANL	.285
SHT	.404
BRL	.260
HW	.204
C1L	.221
C1A	.215
C1P	.059
C3L	.222
C3W	.181
C5L	.199
C5W	.217
DKL	2.796
DKC	2.424
SIM	.133
AXL	.183
INL	.268
NOT	.000
HPW	.376
FAW	.352
GUW	.169
AIC	1.311
M2C	1.024
M11	1.528

Table 30. Mean value of each character for each population of *Kinosternon scorpioides* females, expressed as a proportion of CL except as described in the text.

	Population										
Character	21	22	23	24	25	26	27	28	29	30	31
CWN	6.125	6.193	6.200	6.714	6.125	6.363	6.315	6.066	6.000	6.000	6.269
CWA	.680	.691	.656	.627	.673	.638	.642	.641	.629	.642	.626
CWP	.669	.679	.663	.642	.658	.635	.638	.633	.624	.631	.629
ABL	.280	.272	.273	.328	.250	.294	.279	.281	.288	.282	.284
AHW	.513	.523	.504	.489	.527	.501	.502	.490	.482	.478	.498
PHW	.464	.462	.446	.428	.461	.456	.455	.428	.404	.421	.440
TFW	.498	.501	.485	.482	.497	.493	.485	.470	.460	.457	.480
GUL	.165	.160	.149	.171	.175	.159	.159	.157	.176	.171	.163
HUL	.142	.143	.154	.099	.142	.153	.152	.130	.115	.130	.142
PEL	.014	.020	.023	.036	.021	.026	.018	.021	.012	.009	.025
FEL	.035	.036	.060	.028	.063	.039	.036	.043	.035	.027	.047
ANL	.314	.316	.299	.300	.302	.329	.335	.319	.329	.326	.331
SHT	.477	.487	.446	.390	.453	.483	.480	.425	.437	.456	.477
BRL	.308	.323	.283	.304	.297	.314	.311	.308	.302	.317	.293
HW	.196	.191	.190	.183	.197	.198	.203	.181	.182	.185	.218
C1L	.221	.215	.230	.199	.235	.221	.225	.219	.199	.200	.221
C1A	.226	.229	.234	.192	.241	.224	.230	.234	.217	.237	.217
C1P	.054	.054	.058	.061	.062	.067	.062	.063	.056	.065	.065
C3L	.235	.253	.223	.223	.238	.237	.235	.235	.228	.231	.236
C3W	.185	.169	.203	.191	.200	.176	.183	.173	.182	.165	.180
C5L	.173	.172	.184	.164	.163	.174	.184	.167	.178	.178	.180
C5W	.205	.206	.221	.209	.202	.215	.229	.205	.210	.219	.223
DKL	3.000	3.096	2.400	2.285	1.000	3.818	3.631	2.333	3.500	3.083	3.615
DKC	3.125	3.129	3.000	2.571	1.250	3.727	3.473	2.166	3.000	3.166	3.038
SIM	.000	.064	.000	.000	.000	.090	.000	.100	.000	.083	.000
AXL	.136	.165	.148	.030	.181	.160	.161	.158	.165	.165	.177
INL	.270	.286	.277	.258	.293	.278	.267	.287	.283	.293	.312
NOT	.004	.000	.000	.002	.000	.000	.000	.000	.000	.000	.000
HPW	.404	.394	.377	.379	.400	.398	.377	.370	.372	.368	.409
FAW	.381	.367	.357	.367	.372	.365	.355	.340	.335	.350	.360
GUW	.202	.153	.164	.178	.174	.179	.165	.157	.161	.153	.166
AIC	.000	.032	.000	.000	1.000	.000	.000	.066	.000	.083	.230
M2C	.875	1.000	2.000	.571	1.500	1.181	1.315	1.766	1.833	2.000	1.192
M11	1.750	1.903	1.800	2.000	1.875	1.727	1.789	1.333	1.666	1.250	1.038

Table 30 (continued)

	Population				
	32	33	34	35	36
Character					
CWN	6.333	6.000	6.238	5.867	6.000
CWA	.683	.655	.664	.655	.670
CWP	.695	.663	.674	.652	.661
ABL	.252	.241	.280	.317	.302
AHW	.523	.519	.522	.524	.519
PHW	.486	.467	.476	.465	.462
TFW	.522	.509	.507	.501	.503
GUL	.169	.164	.153	.163	.165
HUL	.139	.163	.144	.154	.161
PEL	.040	.012	.031	.019	.014
FEL	.063	.056	.035	.026	.033
ANL	.305	.317	.311	.317	.306
SHT	.451	.449	.441	.470	.454
BRL	.261	.257	.257	.277	.275
HW	.200	.199	.197	.201	.199
C1L	.225	.232	.217	.232	.219
C1A	.224	.241	.202	.217	.215
C1P	.062	.062	.062	.059	.044
C3L	.225	.233	.231	.233	.232
C3W	.208	.189	.201	.197	.178
C5L	.186	.171	.181	.188	.192
C5W	.217	.207	.214	.211	.235
DKL	2.083	3.250	2.000	2.547	2.285
DKC	1.583	1.750	1.333	2.113	1.714
SIM	.333	.000	.285	.339	.142
AXL	.185	.143	.263	.230	.192
INL	.298	.224	.290	.297	.294
NOT	.001	.000	.002	.000	.003
HPW	.390	.512	.349	.405	.398
FAW	.393	.346	.369	.380	.399
GUW	.183	.173	.175	.169	.173
AIC	1.666	.750	2.000	1.792	1.571
M2C	1.166	1.750	.380	.773	.714
MI1	1.583	1.250	.857	.981	1.714

37	38	39	40	42	43
5.888	6.590	6.428	6.176	5.611	5.833
.662	.638	.644	.616	.626	.627
.651	.646	.659	.623	.598	.618
.302	.281	.279	.277	.310	.307
.519	.492	.491	.463	.505	.498
.450	.427	.421	.390	.441	.434
.492	.458	.456	.423	.477	.472
.165	.158	.159	.173	.167	.168
.138	.137	.119	.096	.159	.129
.028	.025	.034	.025	.011	.024
.044	.044	.058	.068	.022	.029
.299	.297	.269	.265	.312	.311
.449	.419	.420	.407	.455	.450
.264	.254	.248	.260	.279	.279
.204	.199	.209	.207	.203	.197
.228	.210	.216	.211	.243	.227
.196	.206	.214	.219	.222	.218
.059	.069	.059	.060	.051	.059
.227	.225	.224	.229	.230	.229
.171	.180	.181	.187	.188	.188
.180	.178	.181	.177	.181	.183
.200	.208	.213	.195	.207	.208
3.055	2.454	2.857	2.764	2.888	2.611
2.722	1.727	2.714	2.705	2.444	2.055
.444	.045	.000	.176	.305	.500
.185	.193	.165	.173	.221	.188
.295	.269	.280	.271	.298	.295
.000	.000	.010	.003	.000	.001
.396	.344	.381	.372	.387	.400
.386	.371	.376	.323	.370	.375
.178	.171	.183	.177	.168	.161
1.833	2.000	2.000	1.941	1.416	1.444
.222	.772	.714	.764	1.083	1.111
1.111	1.636	1.571	1.823	1.250	.944

Table 30 (continued)

Character	Population 44	45	46	47	48
CWN	6.000	6.416	6.500	7.000	6.000
CWA	.689	.627	.604	.632	.625
CWP	.668	.636	.617	.671	.647
ABL	.308	.283	.279	.312	.280
AHW	.553	.453	.430	.476	.443
PHW	.484	.391	.377	.421	.397
TFW	.521	.418	.399	.445	.404
GUL	.171	.179	.155	.179	.155
HUL	.142	.082	.101	.117	.099
PEL	.021	.042	.034	.023	.043
FEL	.021	.078	.096	.101	.084
ANL	.313	.268	.236	.257	.242
SHT	.470	.388	.393	.390	.362
BRL	.294	.264	.270	.289	.272
HW	.210	.211	.201	.195	.196
C1L	.224	.205	.204	.218	.196
C1A	.217	.204	.195	.195	.221
C1P	.052	.061	.063	.070	.071
C3L	.240	.216	.232	.234	.224
C3W	.198	.203	.199	.187	.195
C5L	.204	.179	.160	.164	.155
C5W	.233	.204	.170	.203	.202
DKL	3.000	2.750	2.833	3.000	2.666
DKC	2.750	2.166	3.000	2.000	2.666
SIM	.000	.000	.000	.000	.333
AXL	.190	.149	.168	.164	.158
INL	.286	.306	.267	.257	.270
NOT	.000	.014	.019	.023	.017
HPW	.414	.373	.340	.382	.334
FAW	.398	.291	.301	.343	.315
GUW	.171	.169	.160	.140	.166
AIC	2.000	2.000	2.000	2.000	2.000
M2C	1.250	.750	.500	.000	2.000
M11	1.750	1.500	1.000	2.000	2.000

49	50	52	53	54	Overall Means
6.000	7.000	7.000	7.000	7.000	6.127
.594	.633	.607	.630	.617	.646
.613	.650	.643	.659	.649	.643
.286	.271	.282	.297	.269	.289
.399	.453	.452	.449	.493	.501
.373	.384	.376	.398	.406	.442
.402	.393	.406	.427	.439	.478
.152	.147	.153	.152	.176	.163
.108	.103	.109	.101	.093	.137
.021	.019	.022	.029	.023	.022
.082	.084	.080	.094	.121	.042
.211	.250	.240	.224	.259	.307
.365	.382	.377	.355	.407	.448
.269	.269	.269	.282	.259	.284
.199	.192	.202	.210	.183	.199
.195	.229	.209	.188	.234	.221
.207	.227	.195	.202	.209	.219
.065	.065	.073	.050	.086	.060
.223	.222	.221	.217	.230	.232
.175	.205	.186	.181	.173	.186
.165	.164	.168	.166	.166	.178
.206	.212	.182	.217	.189	.210
2.666	3.333	3.666	4.000	4.000	2.790
3.666	4.000	3.666	4.000	4.000	2.495
.333	.000	.000	.000	.000	.168
.159	.161	.147	.166	.149	.184
.266	.272	.259	.289	.263	.287
.023	.009	.011	.029	.009	.000
.344	.354	.377	.369	.386	.385
.308	.255	.291	.304	.302	.361
.154	.162	.160	.159	.190	.168
2.000	2.000	2.000	2.000	2.000	1.120
1.000	1.000	.000	.000	1.000	1.021
2.000	1.000	1.666	2.000	1.000	1.391

Table 31. Standard deviations of each character for each population of *Kinosternon scorpioides* males.

Character	Population 21	22	23	24	25	26	27	28	29	30	31
CWN	1.032	.503	.873	.353	.816	.577	.836	.722	.389	.000	1.032
CWA	.016	.024	.015	.027	.028	.030	.015	.023	.015	.020	.018
CWP	.024	.021	.018	.026	.030	.036	.022	.016	.015	.013	.016
ABL	.015	.015	.011	.012	.028	.007	.018	.010	.007	.010	.015
AHW	.010	.017	.022	.020	.031	.027	.016	.022	.014	.016	.012
PHW	.015	.013	.020	.019	.038	.015	.021	.017	.016	.014	.018
TFW	.013	.011	.018	.015	.028	.013	.021	.014	.009	.008	.008
GUL	.022	.011	.016	.016	.016	.012	.003	.017	.017	.010	.012
HUL	.025	.024	.024	.018	.038	.010	.008	.020	.017	.006	.009
PEL	.015	.014	.017	.014	.019	.006	.010	.008	.009	.004	.011
FEL	.010	.015	.017	.014	.023	.020	.034	.015	.012	.006	.013
ANL	.010	.015	.020	.022	.013	.001	.024	.013	.014	.015	.023
SHT	.050	.028	.026	.014	.025	.022	.024	.053	.011	.011	.019
BRL	.010	.010	.034	.013	.015	.013	.009	.012	.010	.018	.020
HW	.009	.010	.011	.005	.010	.004	.009	.006	.008	.007	.014
C1L	.018	.013	.014	.013	.016	.006	.004	.011	.012	.004	.011
C1A	.023	.017	.012	.021	.023	.020	.014	.015	.021	.007	.010
C1P	.009	.006	.007	.004	.007	.014	.009	.009	.005	.010	.006
C3L	.022	.012	.007	.010	.012	.018	.016	.012	.007	.017	.010
C3W	.016	.011	.010	.011	.020	.004	.022	.012	.008	.014	.013
C5L	.018	.012	.014	.015	.019	.010	.019	.024	.012	.012	.010
C5W	.017	.015	.018	.020	.034	.029	.025	.022	.015	.015	.019
DKL	.636	.550	.924	.353	1.414	1.154	.447	.596	.492	.000	.421
DKC	.836	.690	.504	.353	1.366	1.154	.447	.595	.668	.500	1.032
SIM	.408	.000	.000	.000	.408	.577	.547	.314	.288	.000	.000
AXL	.024	.018	.078	.000	.085	.015	.010	.020	.021	.029	.228
INL	.020	.019	.083	.019	.015	.026	.006	.018	.019	.014	.019
NOT	.006	.000	.000	.021	.000	.000	.003	.000	.000	.000	.000
HPW	.011	.014	.147	.022	.022	.006	.018	.014	.008	.013	.024
FAW	.022	.014	.059	.022	.030	.018	.009	.013	.009	.014	.101
GUW	.029	.011	.016	.015	.007	.022	.011	.019	.007	.013	.011
AIC	.408	.408	.404	.000	.816	.000	.000	.503	.288	.000	.000
M2C	.816	.761	.404	.517	1.032	1.154	.894	.000	.288	.957	.707
M11	.816	.508	.467	.000	.000	.577	.894	.661	.792	1.154	.483

Table 31 (continued)

Character	Population 32	33	34	35	36
CWN	.447	.707	.833	.783	.870
CWA	.036	.013	.022	.022	.023
CWP	.032	.014	.022	.023	.026
ABL	.006	.014	.021	.014	.011
AHW	.022	.014	.021	.018	.014
PHW	.023	.008	.021	.019	.022
TFW	.019	.007	.017	.024	.015
GUL	.013	.011	.015	.017	.016
HUL	.024	.009	.014	.017	.018
PEL	.012	.007	.013	.012	.011
FEL	.006	.016	.023	.010	.011
ANL	.011	.020	.018	.014	.013
SHT	.013	.019	.017	.017	.014
BRL	.020	.006	.015	.015	.012
HW	.012	.009	.009	.008	.010
C1L	.013	.013	.013	.012	.010
C1A	.028	.011	.027	.024	.021
C1P	.008	.005	.010	.014	.008
C3L	.011	.008	.011	.012	.014
C3W	.022	.014	.013	.011	.016
C5L	.010	.012	.014	.013	.014
C5W	.016	.025	.021	.016	.017
DKL	1.082	1.708	1.360	.662	.717
DKC	.547	.000	1.045	1.019	.899
SIM	.000	.447	.447	.310	.392
AXL	.092	.066	.081	.102	.025
INL	.044	.066	.055	.094	.019
NOT	.000	.000	.005	.001	.075
HPW	.141	.127	.065	.042	.020
FAW	.154	.058	.047	.038	.046
GUW	.025	.009	.014	.012	.014
AIC	1.095	.894	.350	.587	.000
M2C	1.095	.000	.837	.829	.717
MI1	.894	.447	.736	.524	.000

37	38	39	40	42	43
1.002	1.339	1.732	.894	.700	.816
.028	.018	.007	.023	.021	.017
.026	.015	.015	.026	.023	.018
.014	.008	.008	.014	.018	.013
.017	.016	.009	.018	.020	.013
.026	.017	.012	.016	.024	.023
.023	.014	.005	.018	.074	.021
.016	.011	.002	.010	.018	.016
.022	.021	.009	.014	.016	.016
.014	.012	.013	.013	.011	.011
.015	.010	.016	.017	.011	.011
.017	.016	.012	.021	.014	.019
.020	.011	.032	.012	.024	.027
.014	.011	.009	.015	.028	.014
.010	.012	.007	.011	.007	.006
.019	.008	.012	.013	.016	.014
.029	.010	.015	.018	.022	.019
.010	.009	.013	.012	.013	.008
.013	.011	.008	.014	.038	.016
.017	.010	.006	.010	.014	.019
.017	.012	.016	.015	.018	.015
.020	.018	.016	.026	.019	.016
.817	.548	.500	.471	.592	.602
1.177	1.092	.957	.548	1.269	1.000
.371	.235	1.154	.000	.655	.478
.058	.126	.011	.012	.113	.128
.049	.099	.007	.016	.063	.066
.087	.005	.010	.017	.002	.111
.027	.082	.008	.022	.104	.062
.068	.077	.023	.018	.063	.096
.011	.010	.014	.017	.016	.020
.648	.000	.000	.323	.803	.629
.827	.840	1.000	.826	.833	.718
.732	.323	.000	.514	.484	.573

Table 31 (continued)

	Population 44	45	46	47	48
Character					
CWN	1.341	1.190	.000	1.000	.894
CWA	.019	.024	.000	.010	.034
CWP	.014	.029	.000	.023	.039
ABL	.020	.007	.000	.002	.011
AHW	.011	.018	.000	.016	.019
PHW	.014	.021	.000	.016	.022
TFW	.011	.020	.000	.014	.014
GUL	.014	.013	.000	.006	.011
HUL	.022	.020	.000	.021	.010
PEL	.008	.013	.000	.005	.010
FEL	.005	.014	.000	.019	.022
ANL	.011	.015	.000	.017	.016
SHT	.012	.020	.000	.005	.021
BRL	.013	.010	.000	.011	.014
HW	.013	.012	.000	.005	.012
C1L	.017	.011	.000	.016	.014
C1A	.010	.016	.000	.017	.018
C1P	.008	.011	.000	.006	.009
C3L	.008	.018	.000	.012	.017
C3W	.017	.014	.000	.021	.009
C5L	.013	.012	.000	.016	.016
C5W	.005	.017	.000	.012	.011
DKL	.836	1.400	.000	1.000	1.224
DKC	.836	.925	.000	1.000	1.303
SIM	.894	.000	.000	.577	.894
AXL	.012	.055	.000	.009	.011
INL	.033	.078	.000	.005	.026
NOT	.011	.009	.000	.014	.007
HPW	.011	.097	.000	.011	.014
FAW	.018	.070	.000	.004	.008
GUW	.003	.015	.000	.002	.014
AIC	.894	.400	.000	.000	.000
M2C	1.095	.627	.000	.000	.894
M11	.000	.276	.000	.000	.000

49	50	51	52	53	54
.000	1.356	1.154	.000	.000	.000
.010	.012	.017	.008	.019	.000
.014	.025	.021	.000	.014	.000
.008	.010	.005	.012	.021	.000
.015	.012	.006	.007	.008	.000
.007	.021	.015	.016	.022	.000
.018	.020	.017	.013	.019	.000
.008	.012	.007	.008	.004	.000
.001	.024	.012	.012	.003	.000
.003	.017	.009	.003	.012	.000
.015	.017	.012	.000	.070	.000
.031	.018	.031	.017	.028	.000
.008	.014	.008	.024	.001	.000
.003	.011	.007	.003	.005	.000
.000	.023	.015	.012	.003	.000
.021	.009	.016	.007	.012	.000
.019	.016	.041	.003	.012	.000
.017	.012	.016	.008	.010	.000
.006	.007	.007	.001	.008	.000
.004	.009	.001	.002	.008	.000
.000	.011	.008	.020	.007	.000
.014	.019	.020	.019	.006	.000
.707	.534	.577	.707	.000	.000
.707	.517	.577	.000	.000	.000
.000	.000	.000	.000	.000	.000
.007	.010	.020	.009	.000	.000
.008	.012	.015	.008	.004	.000
.013	.010	.008	.018	.048	.000
.024	.015	.018	.007	.002	.000
.016	.011	.009	.003	.014	.000
.013	.018	.007	.019	.014	.000
.000	.000	.000	.000	.000	.000
.000	.991	1.154	.000	.000	.000
.000	.353	1.154	1.414	.000	.000

Table 32. Standard deviations of each character for each population of *Kinosternon scorpioides* females.

Character	Population 21	22	23	24	25	26	27	28	29	30	31
CWN	.353	.401	.447	.755	.353	.504	.582	.365	.000	.426	.535
CWA	.029	.019	.037	.026	.022	.024	.019	.018	.016	.020	.019
CWP	.020	.017	.018	.031	.027	.026	.020	.019	.011	.016	.018
ABL	.013	.012	.048	.012	.025	.022	.014	.014	.016	.012	.012
AHW	.016	.013	.018	.016	.017	.020	.016	.012	.016	.016	.019
PHW	.017	.017	.022	.021	.016	.023	.018	.018	.013	.015	.019
TFW	.023	.013	.020	.020	.021	.019	.020	.016	.012	.010	.016
GUL	.016	.022	.025	.015	.009	.016	.018	.016	.021	.010	.015
HUL	.027	.024	.031	.025	.018	.017	.019	.019	.017	.014	.015
PEL	.013	.016	.014	.018	.013	.013	.017	.014	.013	.009	.014
FEL	.013	.016	.010	.010	.025	.023	.019	.018	.020	.013	.023
ANL	.036	.015	.019	.017	.020	.016	.018	.020	.020	.012	.014
SHT	.044	.014	.043	.021	.022	.028	.027	.030	.014	.016	.022
BRL	.034	.015	.011	.009	.016	.008	.014	.013	.012	.015	.012
HW	.008	.008	.014	.009	.006	.008	.015	.006	.003	.005	.012
C1L	.013	.012	.027	.017	.023	.013	.018	.016	.007	.008	.016
C1A	.022	.019	.014	.022	.021	.023	.016	.020	.020	.011	.020
C1P	.012	.006	.009	.010	.004	.014	.008	.008	.007	.009	.008
C3L	.029	.011	.010	.012	.019	.015	.012	.015	.007	.009	.020
C3W	.027	.012	.026	.019	.019	.017	.013	.018	.010	.009	.012
C5L	.008	.024	.018	.011	.016	.013	.018	.013	.010	.012	.011
C5W	.019	.019	.026	.008	.035	.010	.016	.023	.017	.017	.023
DKL	1.069	.597	.547	.755	.534	.404	.597	.884	.547	.514	.571
DKC	.991	.618	.707	.534	.707	.467	.841	.874	.894	.577	1.341
SIM	.000	.359	.000	.000	.000	.301	.000	.402	.000	.288	.000
AXL	.025	.024	.040	.080	.031	.033	.013	.017	.025	.030	.110
INL	.024	.025	.013	.016	.014	.015	.020	.023	.025	.012	.149
NOT	.011	.000	.143	.005	.000	.000	.004	.004	.000	.000	.000
HPW	.038	.015	.014	.014	.017	.022	.020	.016	.013	.012	.142
FAW	.026	.016	.012	.025	.012	.014	.015	.018	.008	.013	.059
GUW	.101	.012	.011	.011	.019	.014	.016	.012	.016	.011	.010
AIC	.000	.179	.000	.000	1.069	.000	.000	.365	.000	.288	.651
M2C	.991	.966	.000	.975	.925	.981	.820	.568	.408	.000	.749
MII	.462	.396	.447	.000	.353	.646	.535	.844	.816	.965	.527

Table 32 (continued)

Character	Population 32	33	34	35	36
CWN	.651	.000	.538	.556	.000
CWA	.021	.022	.017	.025	.020
CWP	.026	.022	.019	.022	.018
ABL	.018	.016	.028	.015	.021
AHW	.017	.025	.018	.020	.025
PHW	.021	.012	.022	.019	.014
TFW	.022	.018	.022	.014	.012
GUL	.023	.015	.016	.018	.014
HUL	.021	.015	.026	.020	.012
PEL	.020	.014	.015	.013	.010
FEL	.012	.004	.024	.013	.012
ANL	.020	.019	.023	.016	.010
SHT	.017	.032	.022	.026	.030
BRL	.014	.030	.014	.016	.019
HW	.005	.005	.007	.007	.007
C1L	.010	.020	.025	.014	.017
C1A	.022	.015	.026	.023	.014
C1P	.006	.006	.018	.009	.014
C3L	.011	.012	.008	.011	.014
C3W	.028	.008	.014	.017	.016
C5L	.013	.018	.012	.019	.015
C5W	.016	.015	.021	.017	.015
DKL	.514	.947	.774	.748	.407
DKC	.792	.500	1.110	1.187	.755
SIM	.651	.000	.560	.648	.377
AXL	.014	.090	.150	.118	.013
INL	.014	.078	.138	.085	.007
NOT	.003	.000	.070	.000	.005
HPW	.022	.218	.128	.087	.020
FAW	.020	.094	.103	.075	.014
GUW	.014	.021	.014	.010	.011
AIC	.651	.957	.000	.494	.786
M2C	.834	.500	.589	.800	.951
M11	.668	.957	.727	.604	.755

37	38	39	40	42	43
.582	.666	.975	.528	1.076	1.581
.024	.021	.023	.020	.022	.027
.026	.020	.023	.020	.105	.022
.018	.019	.012	.015	.017	.013
.018	.015	.016	.017	.020	.021
.022	.020	.017	.019	.019	.017
.027	.020	.019	.019	.017	.017
.020	.014	.020	.029	.016	.012
.027	.018	.029	.019	.018	.024
.020	.014	.015	.011	.012	.013
.020	.012	.018	.020	.011	.016
.015	.018	.029	.021	.011	.020
.025	.027	.042	.021	.026	.025
.020	.014	.018	.014	.014	.013
.008	.006	.011	.010	.008	.013
.021	.012	.008	.013	.014	.020
.024	.027	.016	.018	.021	.033
.008	.006	.012	.009	.010	.015
.010	.014	.014	.013	.014	.020
.013	.013	.017	.013	.015	.022
.013	.019	.004	.013	.014	.013
.028	.023	.014	.017	.014	.019
.725	.595	.690	.831	.747	.697
1.127	1.120	1.253	.919	1.106	.872
.511	.213	.000	.528	.668	.707
.020	.091	.008	.012	.088	.037
.014	.091	.020	.019	.090	.039
.002	.013	.007	.006	.002	.005
.019	.070	.022	.012	.037	.069
.017	.073	.018	.022	.080	.038
.013	.012	.012	.019	.011	.012
.514	.000	.000	.242	.731	.855
.548	.812	.951	.903	.874	.963
.963	.657	.534	.392	.554	.872

Table 32 (continued)

	Population									
Character	44	45	46	47	48	49	50	52	53	54
CWN	.000	.900	.836	.000	1.000	.000	1.000	1.000	.000	1.414
CWA	.015	.030	.020	.000	.018	.021	.035	.033	.000	.024
CWP	.026	.027	.012	.000	.008	.023	.024	.031	.000	.002
ABL	.026	.012	.020	.000	.002	.009	.012	.014	.000	.020
AHW	.018	.021	.019	.000	.036	.042	.017	.016	.000	.014
PHW	.020	.022	.019	.000	.012	.015	.029	.015	.000	.000
TFW	.020	.013	.010	.000	.023	.023	.019	.002	.000	.016
GUL	.011	.013	.022	.000	.008	.020	.023	.008	.000	.015
HUL	.019	.021	.015	.000	.004	.009	.016	.011	.000	.005
PEL	.008	.014	.012	.000	.004	.001	.003	.004	.000	.015
FEL	.008	.014	.020	.000	.016	.022	.011	.018	.000	.062
ANL	.002	.017	.021	.000	.008	.018	.033	.013	.000	.006
SHT	.041	.027	.016	.000	.006	.021	.033	.006	.000	.019
BRL	.017	.011	.019	.000	.002	.013	.024	.004	.000	.016
HW	.009	.010	.007	.000	.005	.003	.005	.006	.000	.003
C1L	.014	.016	.012	.000	.019	.023	.010	.024	.000	.029
C1A	.008	.022	.010	.000	.023	.033	.013	.030	.000	.013
C1P	.004	.010	.006	.000	.007	.018	.006	.007	.000	.004
C3L	.012	.021	.008	.000	.016	.002	.006	.006	.000	.015
C3W	.011	.019	.013	.000	.020	.015	.008	.008	.000	.001
C5L	.006	.030	.012	.000	.004	.009	.025	.021	.000	.011
C5W	.012	.016	.020	.000	.016	.010	.014	.007	.000	.024
DKL	.816	1.055	.408	.000	1.154	.577	.577	.577	.000	.000
DKC	.957	.717	.632	.000	1.154	.577	.000	.577	.000	.000
SIM	.000	.000	.000	.000	.577	.577	.000	.000	.000	.000
AXL	.026	.064	.013	.000	.000	.013	.023	.009	.000	.007
INL	.016	.060	.013	.000	.017	.020	.024	.010	.000	.001
NOT	.000	.029	.012	.000	.004	.024	.014	.006	.000	.013
HPW	.006	.097	.013	.000	.025	.018	.044	.005	.000	.019
FAW	.030	.074	.024	.000	.013	.011	.084	.013	.000	.047
GUW	.009	.026	.012	.000	.008	.021	.018	.003	.000	.013
AIC	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
M2C	.957	.866	.836	.000	.000	1.000	1.000	.000	.000	1.414
MI1	.500	.674	.894	.000	.000	.000	1.000	.577	.000	1.414

Table 33. Within populations correlation coefficients for <u>Kinosternon scorpioides</u> males (* = significant at .05 level, ** = significant at .01 level).

Character	CWN	CWA	CWP	ABL	AHW	PHW	TFW	GUL	HUL	PEL	FEL
CWN	1.000										
CWA	-.136	1.000									
CWP	.247	.760**	1.000								
ABL	.145	.082	.162	1.000							
AHW	-.032	.534**	.485**	.058	1.000						
PHW	.173	.603**	.715**	.120	.603**	1.000					
TFW	.117	.309	.428*	.074	.313	.457**	1.000				
GUL	-.085	-.119	-.107	-.090	.037	-.093	-.070	1.000			
HUL	.018	.218	.252	-.054	.282	.318	.141	-.524**	1.000		
PEL	.107	.021	.103	.069	-.103	-.009	.040	-.161	-.441*	1.000	
FEL	-.055	.094	.083	-.181	-.021	.006	.060	.002	-.016	.094	1.000
ANL	.018	.105	.091	-.044	.298	.243	.091	.091	.092	-.079	-.521**
SHT	.046	.257	.299	.082	.256	.353*	.164	.024	.148	.017	-.021
BRL	-.056	.224	.175	.337	.210	.226	.070	-.172	.151	-.070	-.044
HW	.037	.198	.136	.008	.187	.229	.112	.139	-.012	.003	-.070
C1L	-.054	.238	.260	-.053	.220	.264	.048	-.010	.154	.000	.059
C1A	-.044	.141	.159	-.005	.078	.139	.086	-.036	.134	-.022	.085
C1P	-.079	.050	-.011	-.157	.003	.005	-.113	.046	-.075	.047	.030
C3L	-.000	-.017	.027	.052	.012	.075	.087	-.029	-.061	.075	-.028
C3W	-.000	.293	.259	.010	.162	.205	.044	-.086	.065	.095	.005
C5L	.033	-.094	-.135	.034	-.029	-.109	-.073	.034	-.040	.035	.023
C5W	.146	.024	.082	.058	.005	-.039	-.055	-.020	.066	.004	.002
DKL	.101	-.115	-.039	.157	-.022	-.050	-.046	.038	-.063	.011	.012
DKC	.099	-.065	.018	.048	-.038	.008	-.057	.085	-.062	-.048	.030
SIM	-.064	-.034	-.008	.073	-.028	-.031	.054	.044	-.039	-.034	.028
AXL	-.024	.115	.080	.005	.082	.067	.097	-.058	.081	-.031	-.003
INL	-.045	.067	.059	.167	.073	.113	.082	-.005	.007	.006	-.011
NOT	-.013	.011	.006	-.041	-.001	.050	.028	.044	-.059	.061	.000
HPW	.043	.026	.064	.023	.133	.119	.069	.033	.038	-.037	.040
FAW	.010	.061	.053	.047	.098	.145	.085	-.039	.135	-.093	-.094
GUW	.065	.068	.167	.076	.120	.131	.049	.126	.052	-.031	.071
AIC	.015	-.000	.020	.031	-.084	.008	.113	-.053	-.050	.078	.080
M2C	-.044	-.024	-.025	-.050	-.060	-.047	-.034	-.061	.061	-.049	.028
M11	-.031	-.052	-.075	-.022	-.058	-.106	-.018	-.037	-.022	.062	.088

Table 33 (continued)

Character	ANL	SHT	BRL	HW	C1L
ANL	1.000				
SHT	.181	1.000			
BRL	.074	.015	1.000		
HW	.134	.273	-.023	1.000	
C1L	.116	.182	.029	-.077	1.000
C1A	-.061	.048	.103	.010	.285
C1P	.079	.078	-.092	.157	-.029
C3L	.003	.158	-.001	.128	.020
C3W	.044	.293	-.002	.272	.060
C5L	-.052	-.066	-.048	.115	-.348*
C5W	-.056	-.048	.019	.060	-.238
DKL	-.113	.051	-.014	-.107	.058
DKC	-.076	.097	-.064	-.178	.081
SIM	.023	-.008	.084	-.037	-.102
AXL	.000	.033	.042	.010	.066
INL	.001	.008	.138	-.004	.016
NOT	-.103	-.045	.029	.014	.016
HPW	.025	.080	.019	.035	.058
FAW	.109	.127	.010	.062	.012
GUW	-.032	.115	.095	.087	.077
AIC	-.074	.114	-.113	.005	-.136
M2C	-.088	-.056	.000	-.038	.018
MI1	-.157	-.113	.135	-.079	-.066

C1A	C1P	C3L	C3W	C5L	C5W
1.000					
.009	1.000				
.013	.020	1.000			
.041	.179	.101	1.000		
-.174	-.019	-.166	-.019	1.000	
-.095	-.016	-.241	.003	.510 **	1.000
-.012	-.134	-.031	-.107	-.045	.050
.001	-.061	-.007	-.124	-.093	.006
.010	-.016	.026	-.008	.096	.050
.011	.011	-.035	.061	.064	.033
.038	.014	-.027	.034	.008	-.040
-.017	.016	.048	-.056	-.123	-.061
.038	.068	.005	.001	.011	.014
.006	.064	.015	-.026	.000	-.024
.096	.022	-.049	.094	-.138	.011
-.053	.097	.096	.091	.041	-.032
.589 **	.017	.025	.025	-.047	-.025
.039	-.107	-.000	-.073	.210	.207

Table 33 (continued)

	Character				
	DKL	DKC	SIM	AXL	INL
Character					
DKL	1.000				
DKC	.489 **	1.000			
SIM	-.088	-.049	1.000		
AXL	-.169	-.442 **	-.008	1.000	
INL	.014	-.083	-.010	.039	1.000
NOT	.022	.007	-.028	.036	-.030
HPW	.129	.140	-.087	-.020	-.111
FAW	-.050	.146	-.032	-.178	.111
GUW	.162	.073	-.064	.084	.101
AIC	-.003	-.045	.087	.032	.081
M2C	-.072	-.013	.067	-.069	-.024
M11	.089	.063	-.053	-.048	.037

	M11
M11	1.000

NOT	HPW	FAW	GUW	AIC	M2C
1.000					
.004	1.000				
-.011	.070	1.000			
.004	.098	.020	1.000		
-.053	-.091	.008	.009	1.000	
-.029	-.035	.006	-.085	-.034	1.000
-.040	-.006	-.016	-.016	-.021	.057

Table 34. Within populations correlation coefficients for Kinosternon scorpioides females (* = significant at .05 level, ** = significant at .01 level).

Character	CWN	CWA	CWP	ABL	AHW	PHW	TFW	GUL	HUL	PEL	FEL
CWN	1.000										
CWA	-.172	1.000									
CWP	.081	.321	1.000								
ABL	-.059	.022	-.090	1.000							
AHW	-.058	.522 **	.233	.150	1.000						
PHW	.104	.464 **	.417 *	.144	.499 **	1.000					
TFW	.084	.444 *	.374 *	.184	.558 **	.745 **	1.000				
GUL	-.063	.096	.036	.101	.260	.098	.101	1.000			
HUL	.056	.062	-.008	.010	.128	.155	.172	-.461*	1.000		
PEL	.011	.041	.092	-.202	-.095	.000	-.089	-.035	-.535**	1.000	
FEL	-.020	.033	.042	-.328	-.110	-.125	-.127	-.101	-.069	.184	1.000
ANL	.002	.071	.024	.108	.283	.248	.332	.154	.128	-.144	-.651 **
SHT	.008	.256	.135	.273	.339	.392 *	.444*	.141	.158	-.162	-.242
BRL	-.103	.310	.008	.476 **	.293	.155	.242	.079	.019	-.161	-.221
HW	-.022	.249	.077	-.007	.151	.272	.228	.044	.104	.068	.049
C1L	-.032	.193	.137	-.197	.242	.185	.186	.071	.125	.011	.048
C1A	-.025	.115	.031	.024	.109	.163	.166	-.004	.083	-.026	.022
C1P	.081	.083	.062	-.080	-.026	.093	.034	-.019	.004	.000	.099
C3L	-.010	.136	-.066	.166	.053	.094	.109	-.005	.031	.007	-.081
C3W	.018	.338	.207	-.052	.112	.232	.143	-.060	.015	.182	.113
C5L	.104	-.061	.078	.048	-.087	.004	-.027	-.093	.062	-.057	-.003
C5W	.094	.053	.122	-.010	-.009	.045	-.008	-.096	.023	.000	.057
DKL	.001	-.092	.032	-.005	-.082	-.029	-.016	.003	.034	-.041	.034
DKC	.002	-.055	.045	-.054	-.078	-.019	-.013	-.007	-.002	.013	.064
SIM	-.031	.080	.034	-.003	.061	-.033	-.070	.037	.017	.023	-.022
AXL	-.015	.045	.026	.045	.114	.065	.071	.031	.070	.019	-.023
INL	.034	.089	.093	-.016	.119	.130	.098	.064	-.044	.017	.066
NOT	-.037	.174	.065	-.169	.193	.133	.089	-.078	.112	-.022	.029
HPW	-.015	.025	.006	.031	.040	-.034	.013	.075	-.039	-.015	.003
FAW	-.031	.081	.082	.057	.096	.105	.181	.043	.002	.042	-.052
GUW	-.044	.049	.090	-.076	.085	.104	.049	.122	-.033	.078	.111
AIC	-.032	.086	.038	.005	.023	-.090	-.112	.070	-.066	.064	.038
M2C	-.031	-.054	-.105	-.041	-.015	-.039	.050	-.033	.052	-.056	-.059
M11	.098	-.020	-.074	-.007	-.024	-.033	.028	-.015	.050	-.116	.036

Table 34 (continued)

Character	ANL	SHT	BRL	HW	C1L
ANL	1.000				
SHT	.418*	1.000			
BRL	.198	.225	1.000		
HW	.098	.354*	-.016	1.000	
C1L	.082	.058	-.073	.068	1.000
C1A	-.020	.028	.040	.109	.282
C1P	-.059	-.011	-.188	.277	.009
C3L	.122	.248	.180	.105	-.033
C3W	-.087	.058	-.030	.190	-.033
C5L	-.057	.022	-.011	.016	-.260
C5W	-.079	.042	-.026	.026	-.238
DKL	-.057	-.011	-.069	-.110	.175
DKC	-.029	.061	-.037	-.128	.170
SIM	.090	-.009	.120	-.081	-.042
AXL	.044	.027	.019	-.004	.064
INL	-.033	.050	.031	.048	.037
NOT	.005	.030	.033	.072	.158
HPW	-.015	-.017	-.063	.051	.036
FAW	.052	.110	.004	.124	-.023
GUW	-.174	-.085	-.211	.121	.141
AIC	-.105	-.049	-.148	-.060	.002
M2C	.073	-.029	.065	.028	.001
M11	-.123	.029	.047	-.056	-.155

C1A	C1P	C3L	C3W	C5L	C5W
1.000					
.214	1.000				
.104	.012	1.000			
.186	.287	.085	1.000		
-.105	.024	-.160	-.030	1.000	
-.226	.061	-.188	.044	.435 *	1.000
-.001	-.093	-.075	-.227	.007	-.063
.003	-.146	-.080	-.092	.019	.021
-.104	-.052	.009	.074	.067	.012
.031	-.114	.008	-.003	-.058	-.064
.052	.041	.013	.039	.017	.026
.086	.023	-.038	.116	-.030	.046
-.018	.132	-.014	-.007	-.061	-.041
.039	.072	.019	.008	.035	.037
.083	.158	-.140	.175	-.063	.055
-.097	-.023	.009	.019	.047	.060
.578 **	.148	.091	.029	-.086	-.117
-.094	-.140	.030	-.058	.110	.280

Table 34 (continued)

	Character				
	DKL	DKC	SIM	AXL	INL
Character					
DKL	1.000				
DKC	.561 **	1.000			
SIM	-.031	-.129	1.000		
AXL	-.142	-.411 *	.061	1.000	
INL	-.006	-.120	.004	-.087	1.000
NOT	-.153	-.132	.016	.087	.038
HPW	.155	-.013	-.139	-.027	-.153
FAW	-.033	-.056	.056	-.033	-.151
GUW	-.002	.003	-.068	-.046	.009
AIC	.032	-.009	.098	-.009	-.031
M2C	-.135	-.121	.001	-.016	-.025
M11	-.050	-.013	-.042	-.017	.027

	M11
M11	1.000

NOT	HPW	FAW	GUW	AIC	M2C
1.000					
-.020	1.000				
.014	.130	1.000			
.114	.130	.043	1.000		
.008	.083	-.003	.019	1.000	
.034	-.040	.030	-.000	-.112	1.000
-.044	-.024	-.050	-.017	.011	.047

Table 35. Number of specimens assigned to each population by multiple discriminant analysis of Kinosternon scorpioides males.

Number of Specimens Assigned to Population:

Original Population	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	42	43	44	45	46	47	48	49	50	51	52	53	54
21	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	1	21	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	1	0	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	1	1	0	0	1	0	0	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	1	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	2	31	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	2	57	1	2	0	0	0	4	4	0	0	0	0	0	0	0	0	0	0	0

Table 35 (continued)

Number of Specimens Assigned to Population:

Original Population	21	22	23	24	25	26	27	28	38	39	40	42	43	44	45	46
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	12	0	0	0	4	0
42	0	0	0	0	0	0	0	0	1	0	0	33	3	1	0	0
43	0	0	0	0	0	0	0	0	1	0	0	0	14	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
45	0	0	0	0	0	0	0	0	0	0	4	0	0	0	21	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

29	30	31	32	33	34	35	36	37
47	48	49	50	51	52	53	54	
0	0	0	0	0	1	0	15	1
0	0	0	0	0	0	0	0	
0	0	0	0	0	1	3	1	21
0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	
1	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	
0	0	0	0	0	0	4	0	0
0	0	0	0	0	0	0	0	
0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0
0	5	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	
0	0	0	0	0	0	0	0	0
0	0	1	7	0	0	0	0	
0	0	0	0	0	0	0	0	0
0	0	0	0	3	0	0	0	

Table 35 (continued)

Number of Specimens Assigned to Population:

Original Population	21	22	23	24	25	26	27	28	38	39	40	42	43	44	45	46
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

29	47	30	48	31	49	32	50	33	51	34	52	35	53	36	54	37
0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Table 36. Number of specimens assigned to each population by multiple discriminant analysis of Kinosternon scorpioides females.

Number of Specimens Assigned to Population:

Original Population	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
21	5	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
22	0	30	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
23	1	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	1	0
26	0	0	0	0	0	10	1	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	17	0	1	0	1	0	0	0	0	0	0
28	0	2	0	0	1	0	0	25	0	2	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0
31	0	0	0	0	0	0	2	0	0	0	23	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0
33	0	0	0	0	1	0	0	0	0	0	0	0	3	0	0	0	0
34	0	0	1	0	0	0	0	0	0	0	0	2	0	14	3	0	1
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	1	3

Original Population	38	39	40	42	43	44	45	46	47	48	49	50	52	53	54
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	4	5	0	0	0	0	0	0	0	0	0	0

Table 36 (continued)

Original Population	Number of Specimens Assigned to Population:							
	21	22	23	24	25	26	27	28
	38	39	40	42	43	44	45	46
36	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0
	19	1	0	0	1	0	0	0
39	0	0	0	0	0	0	0	0
	1	6	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0
	0	1	15	0	0	0	1	0
42	0	0	0	0	0	0	0	0
	0	0	0	29	3	1	0	0
43	0	0	0	0	0	0	0	0
	1	0	0	3	10	0	0	0
44	0	0	0	0	0	0	0	0
	0	0	0	0	0	4	0	0
45	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	11	1
46	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	6
47	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0

29	30	31	32	33	34	35	36	37
47	48	49	50	52	53	54		
0	0	0	0	0	0	0	7	0
0	0	0	0	0	0	0		
0	0	0	0	0	0	0	1	16
0	0	0	0	0	0	0		
0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0		
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0		
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0		
0	0	0	0	0	0	3	0	0
0	0	0	0	0	0	0		
0	0	1	1	0	0	1	0	1
0	0	0	0	0	0	0		
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0		
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0		
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0		
0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0		
0	0	0	0	0	0	0	0	0
0	3	0	0	0	0	0		
0	0	0	0	0	0	0	0	0
0	0	3	0	0	0	0		
0	0	0	0	0	0	0	0	0
0	0	0	3	0	0	0		
0	0	0	0	0	0	0	0	0
0	0	0	0	3	0	0		

Table 36 (continued)

Number of Specimens Assigned to Population:

Original Population	21	22	23	24	25	26	27	28
	38	39	40	42	43	44	45	46
53	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0

29	30	31	32	33	34	35	36	37
47	48	49	50	52	53	54		
0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0		
0	0	0	0	0	0	2		

Table 37. Summary table of multiple discriminant analysis of *Kinosternon scorpioides* males.

Step	Variable Entered	F Value
1	ANL	43.093
2	AIC	23.557
3	ABL	14.789
4	PHW	11.180
5	CWP	10.579
6	BRL	7.837
7	C1L	7.064
8	HW	7.379
9	C3W	6.187
10	FEL	4.925
11	SHT	4.130
12	C1P	3.521
13	M2C	3.514
14	DKL	3.452
15	M11	3.319
16	CWA	3.310
17	GUL	2.937
18	HUL	3.464
19	C5W	2.862
20	SIM	2.643
21	DKC	2.459
22	AXL	2.297
23	GUW	2.263
24	C5L	2.235
25	PEL	2.200
26	TFW	2.069
27	AHW	1.807
28	C1A	1.546
29	CWN	1.446
30	NOT	1.318
31	FAW	1.298
32	C3L	.995
33	INL	.588
34	HPW	.579

Table 38. Summary table of multiple discriminant analysis of *Kinosternon scorpioides* females.

Step	Variable Entered	F Value
1	AIC	43.379
2	TFW	32.800
3	ABL	14.259
4	HW	12.917
5	BRL	10.594
6	ANL	7.499
7	FEL	6.014
8	C1L	5.423
9	DKL	5.376
10	SHT	4.901
11	CWA	4.374
12	C3W	4.948
13	C1P	4.059
14	HUL	3.363
15	C5W	2.901
16	PEL	2.838
17	NOT	2.728
18	AHW	2.526
19	M11	2.514
20	C1A	2.439
21	GUW	2.259
22	CWN	1.752
23	PHW	1.655
24	GUL	1.654
25	DKC	1.562
26	AXL	1.860
27	CWP	1.338
28	M2C	1.309
29	C5L	1.263
30	SIM	1.164
31	HPW	1.232
32	C3L	.965
33	INL	.744
34	FAW	.449

APPENDIX 2

Specimens Examined

All specimens examined in this study are listed below by species complex (*Kinosternon scorpioides* complex first, *K. leucostomum* second), by population as defined in the text, and by state (México) or country (Central and South America). Each specimen number is preceded by a standard museum or collection acronym. All acronyms are as in Duellman, Fritts, and Leviton (1978), except the following:

CRE - Costa Rican Expedition, University of Southern California, Los Angeles

JBI - John B. Iverson personal collection, Gainesville, Florida

JP - Jorge Perez, Turrialba, Costa Rica

UF - University of Florida, Florida State Museum, Gainesville, Florida

WED - William E. Duellman personal collection, Lawrence, Kansas

Each population designation (number, letter, or combination of numbers and letters) is followed in parentheses by the total number of specimens examined from that population, the total number of males used in the statistical analyses, and the total number of females used in the statistical analyses; for example, "Population 1A (34:13,15)" in which 34 total specimens were examined, 13 males and 15 females were used in the statistical analyses.

Kinosternon scorpioides Complex

Population 1A. (34:13,15)

SONORA: Alamos (27°01'N, 108°56'W), MVZ 50907-10, AMNH 64163-68, ASU 6781; 0.5 mi W Alamos, UU 14279; 3.5 mi W Alamos, JBI 859; Rancho Carrizal, 7 mi W Alamos, UU 14280-81, ASU 6383, 6385-87, 6389-90; 14.8 mi W Alamos, JBI 858; La Esmeralda Ranch, 1.2 mi N Alamos, LACM 105403-04; 8 mi S Alamos, ASU 6547; La Casa de la Huerta, Sierras de Alamos, UU 11853; 4.5 mi W Minas Nuevas (by rd) UA 39891; ca. 23 mi (by rd) E Navajoa, UA 31741; 7.6 mi by rd to Tezapaco NE Esperanza, UA 39889; San Carlos Bay, UC 35122; 14.7 mi S Empalme

(27°58'N, 110°51'W), UIMNH 24456; 28 mi S Navajoa, UC 16145.

SINALOA: 14.7 mi S (by rd) Guasave (25°34'N, 108°27'W), UA 27956; "Culiacán" (locality incorrect; R. L. Bezy, Pers. Comm.), LACM 105396-97.

Population 1b. (98:13,27)

SONORA: Alamos (27°01'N, 108°56'W), AMNH 64161-62, ASU 6075, UU 7677, 11855; 0.8 mi S Alamos, ASU 6545; 4 mi SE Alamos, ASU 6077, 6107; 9 mi SE Alamos, Río Alamos, KU 47589-90, 47592-94; 1 km E Alamos, JBI 862; 8 mi SSE Alamos, Rio Cuchujagui, LACM 105406; ca 2 mi NE Alamos Church, Alamos, UA 39892; La Casa de la Huerta, Sierras de Alamos, UU 11678, 11852, 11854; N slope of Sierras de Alamos, UA 36480; Guiricoba (26°53'N, 106°41'W), MVZ 28937, 50889-902, AMNH 63755-57; Barranca del Cobre, E Guiricoba, LACM 75350; La Aduana (27°03'N, 109°00'W), LACM 105402, UA 38189-90; mine, 1/4 mi NW La Aduana, UA 38705-06; 1/2 mi N La Aduana, UNM 5787, UA 28015, 28019, 28022-23; abandoned mine nr La Aduana, UNM 14492; nr Pilares Mine, UMMZ 79514; 20 mi by rd to Yecora NE Nuri (28°02'N, 109°22'W), UA 38864; 12 mi (by rd) SW Santa Ana de Yecora, UA 39890; 10.5 mi W (by rd) Rosario (27°59'N, 109°20'W), UA 28008-09.

CHIHUAHUA: Milpillas (27°13'N, 108°38'W), UA 28238; vic Milpillas, UA 28141-74; 1.5 mi (by rd to San Antonio) SW Milpillas, UA 39893-94.

SINALOA: Río del Fuerte, 3 mi NNE San Miguel (25°56'N, 109°03'W), KU 63637-46; 13 km NNE Vaca, KU 80772-73.

Population 2. (40:25,15)

SINALOA: Río Sinaloa at Guasave (25°34'N, 108°27'W), AMNH 82142; trib Río Sinaloa, 12 mi E Guasave, UU 7786-818; trib Río Bacaburito, Río Sinaloa, UMMZ 122242; Río Mocorito, La Huerta, LACM 75351; trib Río Mocorito, 0.9 mi S San Benito, UMMZ 122235-39.

Population 3. (157:29,67)

SINALOA: Culiacán (24°48'N, 107°24'W), AMNH 82143, LACM 105394-95; 5.5 mi N Culiacán, LACM 105393; 7.6 mi N Culiacan, UMMZ 121922; 11 mi NW Culiacan, UU 3799-800; Rancho los Pocitos, 14.2 mi N Pericos jct, UA 36511; El Dorado (24°17'N, 107°21'W), KU 45398; 2 km N El Dorado, Laguna Rio Viejo, UU 7678-774, 13007-08; 17 mi ENE El Dorado, Río San Lorenzo, UU 7775-818; 1 mi SE Camino, KU 63633-36; 1-1/2 mi N Badariguato, KU 83423.

Population 4. (75:29,35)

SINALOA: Río Presidio, Villa Union (23°12'N, 106°14'W), UU 7819-24, UMMZ 102625-26; 6 mi NE Villa Union, KU 48557-60; 4 mi S Villa Union, UMMZ 118040-41; Mazatlan (23°13'N, 106°25'W), USNM 12607-08;

Santa Lucia, KU 75648-53, 78977; 5 km SW Santa Lucia, KU 80771; Concordia (23°17'N, 106°04'S), UNM 9998-10009; Concordia, along trib of R Presidio, UNM 102627; 25 km NE Concordia, UU 13282; Presidio, USNM 14084; 0.5 mi S Concepción, KU 63612-32; 1 mi SE, 26 mi NE Villa Union, LACM 105389-90; 12 km W Cuspaderos, KU 78978; Río del Baluarte, 1/2 mi E Rosario (23°00'N, 105°52'W), UU 7825-37.

Population 5. (12:4,7)

SINALOA: 2 mi S Escuinapa, Mex Hwy 15 (22°51'N, 105°48'W), LACM 105391; 5.8 mi S Escuinapa, Mex Hwy 15, LACM 105392; Rio Cañas nr La Concha (20°45'N, 105°34'W), UNM 31024; nr Acaponeta in extreme southern Sinaloa, USNM 45611.

NAYARIT: nr Rosamorada, between Tepic and Acaponeta (22°08'S, 105°12'W), UF 32623; Hwy 15, 2 mi N Acaponeta, UU 7952.

DURANGO: 1/2 mi N Graceros (23°44'S, 104°03'W), KU 68737, 68746-47; NE of Durango (24°02'N, 104°40'W), UMMZ 113699; nr Hacienda Coyotes, UMMZ 113700; Ojode Agua de San Juan, 1 mi N Los Berros, ca 26 mi ESE Durango, UMMZ 129824.

Population 6. (46:17,18)

NAYARIT: San Blas (21°31'N, 105°16'W), KU 62584-87, LACM 105369-77, 105383-86; 4.2 mi NE San Blas, UMMZ 126441; 5 mi NE San Blas, UMMZ 112999; 15 mi N San Blas, UNM 12522; Rio San Cayetano nr Tepic (21°30'N, 104°54'W), AMNH 82144-47; Río de Tepic, 17 mi SE Tepic, UMMZ 118042-44; Rancho Los Armadillos (4.5 E and a little S of Tepic), UMMZ 117139, 118073; Rancho de Tamarillo, 4.5 mi SE Tepic, UMMZ 119140; 223 mi SE Tepic on Hwy 15, LACM 105381; Laguna Sta Maria, 9 km NE Sta María, UMMZ 126145; Lago de San Pedro Luganillas, 12 mi E Compostella (21°14'N, 104°55'W), UU 12097-103, UMMZ 113104; María Madre Island, Los Tres Marías Islands, USNM 24606-10, UU 13285.

JALISCO: Magdalena (20°55'N, 103°57'W), UU 5085-88, AMNH 87650-51, 96577-80; 4.5 mi E Magdalena, UMMZ 104821; 7 mi E Tequilla, AMNH 96588; Mesa Maria de Leon, KU 102993-94; 7 mi S Colotlan, UMMZ 118047.

ZACATECAS: 13 mi SW Zacatecas (22°47'N, 102°35'W), UMMZ 123254; 9 mi W Zacatecas, UMMZ 118048; 3 mi NW Teul, UMMZ 118046, 118054; 2 mi SE Laguna Valderamma, UMMZ 118049-53; 8 mi S Moyahua, UMMZ 118055, CAS 96048-50.

AGUASCALIENTES: 11-1/2 mi E Aguascalientes (21°53'N, 102°17'W), KU 48263; Rincon de Romos, MVZ 67431; Jocoque dam, SU 19692-93; 3/4 mi W Santiago, SU 19697-98; 1 mi W Santiago, SU 19700-01; Rio Panuelo-Aguido, SU 19702-03.

Population 8A. (20:10,7)

JALISCO: Trib Río Ameca, 1 mi W Ameca (20°33'N, 104°02'W), UU 12112-13; Río Ameca, 6 mi E Ameca, UMMZ 102178-84; trib Río Ameca, 2.5 mi E Mascota (20°32'N, 104°49'W), UU 12105-11; 2.3 mi N Ixtapita, UMMZ 113099, 113103; 25 mi N Etzatlan, rd to Magdalena, UMMZ 12224.

NAYARIT: 77 mi SE Tepic, UU 7838.

Population 8B. (5:2,1)

JALISCO: El Tobacco, KU 102995; Arroyo El Arado, rd to Purificación (19°43'N, 104°38'W), UU 12114-17.

Population 9A. (38:18,12)

JALISCO: nr Guadalajara (20°40'N, 103°20'W), UMMZ 117257; Guadalajara Airport, AMNH 87649; 10.1 mi E Guadalajara, UMMZ 99442; 12 mi S Guadalajara, UMMZ 97166; Copalita (± 17 mi NW Guadalajara), UMMZ 113105; Creek at La Huerta (W of Guadalajara), UMMZ 122244; 8.8 mi E Tepatitlan, UMMZ 99444; L Chapala, UMMZ 97170-72; Lake Chapala, 1 mi S Jocotepec (20°18'N, 103°26'W), UMMZ 126440, UU 17449; Granja Azul, Jocotepec, AMNH 96582-83; Lake Chapala at Puente Cofradia, 3 mi W Tuxcueca, UU 17450-59; trib Río Grande de Santiago, UMMZ 113102; 4 mi NE Ocotlan, KU 43639.

MICHOACÁN: 3.4 mi W Jiquilpan (19°59'N, 102°43'W), UMMZ 99431-41; 30.7 mi E Jiquilpan, UMMZ 99445.

Population 9B. (22:8,10)

JALISCO: nr Villa Corona (20°25'N, 103°41'W), AMNH 93247; Lake Atotonilco, Villa Corona, AMNH 96585; Laguna de Atotonilco, 0.5 mi E Villa Corona, UU 12118-19; 13 mi S, 15 mi W Guadalajara, KU 43640-47, 50713; 19 km E Cocula (20°23'N, 103°50'W), KU 95793; 22 km E Cocula, KU 95792; 2 mi S Estipac, AMNH 96581; 2 mi NE Verdia, KU 43632; 2 mi W Acatlan, LACM 37640-44.

Population 10. (153:50,54)

JALISCO: 8 mi NE Union de Tula (19°55'N, 104°16'W), KU 62535-68; 12 mi NE Union de Tula, KU 62569-78; 2 mi SW Union de Tula, KU 62579; Armeria drainage, Union de Tula, BYU 23819-21; 4 mi SW Pihuamo (19°15'N, 103°23'W), KU 62534; 10 mi NE Pihuamo, KU 62580; Rio La Labor, 11 mi E El Grullo, UU 12121-23.

COLIMA: Queseria (19°22'N, 103°35'W), UMMZ 80232-33; Río Colima nr Coquimatlan (19°12'N, 103°48'W), UMMZ 80239-71, 80279-90, 80308-33; Rio Colima, nr Colima, UMMZ 80234-35, 80237; Rio Salada at La Estomcia, UMMZ 80272-78, 80291-07.

Population 11A. (17:7,9)

MICHOACÁN: 6.7 mi S Lake Cuitzeo (19°55'N, 101°05'W), UMMZ 97139-45; Tacicuaro, USNM 108589.

GUANAJUATO: Celaya (20°31'N, 100°37'W), USNM 45902-03, 45942; 6 mi W Celaya, KU 40133; 4 mi N, 5 mi W Leon, KU 39979; trib Rio Turbio, 18.5 mi NW Cueramaro, UU 12083-84.

MÉXICO: Ixtapan de la Sal, UMMZ 118266; 12 mi N Acambay (19°57'N, 99°51'W), UMMZ 118637.

Population 11B. (13:10,0)

DISTRITO FEDERAL: Xochimilco (19°16'N, 99°06'W), UF 40651-63.

Population 12. (25:9,9)

TAMAULIPAS: La Joya de Salas, UMMZ 100116-23, 103188-97, 105471-75; Gallitos (22°53'N, 99°33'W), UMMZ 110959; Rio Chihue at Hwy 101, at village of San Antonio (SW Cd Victoria), 77J175.

Population 13. (46:12,31)

SAN LUIS POTOSÍ: Presa Gonzales Santos, 10 mi SW San Luis Potosí (22°09'N, 100°59'W), UMMZ 109773-76; 4 mi W Bledas, UMMZ 109768-70; 1.8 mi W Bledas, LSUMZ 2481; Laguna Belas, UMMZ 109771; Jesus María, FMNH 2192; San Luis Potosí reservoir, LSUMZ 2484; Luna Media, LSUMZ 7852; Presa Prudentia, LSUMZ 7870; Rio Villeto (Panucho) 9 mi S Santa María del Río, UU 12085; 15.3 mi SE San Juan del Río, UMMZ 118074; Agua del Media, UMMZ 77307-15.

QUERETARO: Cadereyta (20°42'N, 99°49'W), UMMZ 99409-30.

Population 14. (172:43,44)

MICHOACÁN: Coalcomán (18°47'N, 103°09'W), UMMZ 104835-959; Rio Coalcomán, N Coalcomán, UMMZ 104527, 104829-31; ± 2 mi N Coalcomán, UMMZ 104833; SW edge of Coalcomán, UMMZ 104828; Coalcomán, jct Ríos Coalcomán and Chiquita, UMMZ 103937-73; 3 km W Coahuayana, UMMZ 103975; Aguililla (18°44'N, 102°44'N), UMMZ 119588; 1/2 mi W San Pedro Damian, UMMZ 103977; La Puerta de la Play (at Jorullo), UMMZ 105162.

Population 15. (28:13,10)

MICHOACÁN: Capirio, KU 62581-82; 1 mi N Arteaga (18°28'N, 102°25'W), UMMZ 119589; 8 mi S Arteaga, UMMZ 119591; Rio Aguacate, trib to Río Tumbiscatio, 5 mi W Arteago, UMMZ 118045; Apatzingan (19°05'N, 102°21'W), USNM 108733, UMMZ 97189; Arroyo Potzoris, 1 mi E Uruapan, UMMZ 119139; ± 10 mi S Tacambaro, UMMZ 99761; La Huacano rd 10 mi S Ario de Rosales, UMMZ 104822-24; 0.8 mi S Lombardia (19°09'N, 102°02'W), UMMZ 121245-46; 2.5 mi S Lombardia, UMMZ 121247; Los Reyes, USNM 46268; 5.1 mi S Los Reyes, UMMZ 121248-49.

GUERRERO: Colonia Buenos Aires, UMMZ 119592-97; Petacalco, UMMZ 125363; 1.2 mi S Charapan de Leon, UMMZ 112766-68.

Population 16. (62:18.39)

GUERRERO: Acapulco (16°51'N, 99°55'W), USNM 46272; Laguna, 15 mi SE Hwy 200, Acapulco, UU 7846-85; 4-18 mi N Acapulco, UU 7919-20; Lake Coyuca, UMMZ 80964; Coyuca de Benitez, USNM 108729-32; 23 km N Hwy 200, Coyuca, UU 7839-7845; S of El Treinte, 1 mi N Organos, FMNH 116540; nr Xaltinanguis, FMNH 116523; Rio Santiago, KU 87292-93; San Vincente, KU 87294; Mazatlan, FMNH 116524; Pozo, nr Ocotillo, FMNH 116514.

Population 17. (13:10,3)

MEXICO: Cuernavaca (18°55'N, 99°15'W), USNM 108734-39.

MORELOS: Alejandra las Estacas, UMMZ 80790-91; 2.4 mi N Cuautla, UMMZ 99443.

GUERRERO: 11 mi SW Puente de Ixtla, FMNH 116513; 1 mi N Copuyo on Huetanic Rd, FMNH 116487; 4 mi NW Apetlanca, KU 43648; El Mogote, 16 mi S Ixtapan, KU 62583.

Population 18. (39:10,26)

PUEBLA: Puebla (19°03'N, 98°12'W), USNM 108590, 108593, 108609-10, 108614-15, 108617, 108624, 108626, 108628-29, 108631; 3.8 mi SW Puebla, UMMZ 119496; Lago Valsequilla, S of Puebla, UF 20647; Matamoras (18°36'N, 98°28'W), MVZ 76528; 8 mi S Matamoras, CAS 87218; Raboso (18°34'N, 98°26'W), KU 40135-38; Balsas basin, Rio Atoyac, 28 mi S Molcoxac, UU 12086-96.

OAXACA: Huajuapan de Leon (17°48'N, 97°46'W), UMMZ 102173-76, KU 62527; 10 mi N Huajuapan de Leon, UU 7951; 2 mi SW Tlaxiaco, UMMZ 125364-65.

Population 19. (33:12,15)

PUEBLA: San Diego (18°26'N, 97°21'W), UMMZ 88726-30, 89394-95, USNM 108591-92, 108741; La Virgin, N of Tehuacan, UMMZ 88731-48, 89385-87; Cosamaloapam, FMNH 116510, 116537.

Population 20A. (4:2,2)

OAXACA: Oaxaca (17°03'N, 96°43'W), UMMZ 119497; Juchatengo, KU 87297; Rancho San Felipe, LACM 64498-99.

Population 20B. (7:3,3)

OAXACA: 7.2 mi N Pochutla along Mex Hwy 175, UC 48857 (holotype); 7 mi N Pochutla, AMNH 88884 (allotype); Pochutla (15°46'N, 96°28'W), UIMNH 9975 (paratype); 1 km NNW San Gabriel Mixtepec, KU 87296; Chacalapa (between Puerto Angel and Miahuatlán), KU 38209-11.

Population 21. (14:6,7)

VERACRUZ: Veracruz (19°12'N, 96°08'W), UMMZ 89389, USNM 109193, 109203-04; nr city of Veracruz, FMNH 116502, 116504-05; 5 mi S Paso del Toro, UMMZ 122137; 8.4 mi SE Paso del Toro, UMMZ 119601; Cerro Gordo (19°34'N, 96°39'W), USNM 109232; 18 mi NE Huatusco (19°09'N, 96°57'W), UMMZ 103181.

TAMAULIPAS: Río Sabinas, 5 mi NE Gomez Farias (23°03'N, 99°09'W), UMMZ 105476; 6 mi S Antigua Morelos, UMMZ 118635.

SAN LUIS POTOSÍ: Arroyo, 3 mi SSE Ajinche, LSUMZ 2480.

Population 22. (81:24,50)

OAXACA: Tehuantepec (16°20'N, 95°14'W), UMMZ 118631-34, USNM 109105-23; vic Tehuantepec, UMMZ 82226-35; Tehuantepec R., Tehuantepec, UMMZ 82183-224; 12 km NW Tehuantepec, UMMZ 82225; Nisa Pipi, 8 km NW Tehuantepec, UMMZ 82238; 5 leagues S Tehuantepec, Rancharia Lamanga, UMMZ 82236-37; San Mateo del Mar (16°12'N, 95°00'W), USNM 113278; 12 mi NE Juchitan (16°26'N, 95°01'W), UU 7950.

Population 23. (14:11,3)

CHIAPAS: vic of Tonalá (16°04'N, 93°45'W), UU 5149-50, 7624-33; Pijijiapam, UMMZ 119482-83.

Population 24. (23:8,7)

CHIAPAS: Tuxtla Gutierrez (16°45'N, 93°07'W), USNM 7519, 7521, 7523-29; vic Tuxtla Gutierrez, UU 12423; Río Sabinal, vic Tuxtla Gutierrez, UMMZ 119476-81; Berriozabal, UMMZ 119598-600; km 30, 2 km S Santa Isabel, UMMZ 95083; 4 km N Ixtapa, KU 59789-90; 32 km N Arriaga, KU 59791-92.

GUATEMALA: El Reposa (4.2 mi W of La Democracia), Depto Huehuetenango, UMMZ 126300.

Population 25. (17:6,8)

CHIAPAS: 2 km W Acacoyagua (15°21'N, 92°39'W), UMMZ 87747-55; 1 league W Soconusco, UMMZ 87746; 7.3 mi N Puerto Madero, UMMZ 119493.

GUATEMALA: Hacienda Casa Blanca, Depto Retalhuhed, UMMZ 107882-84; Panajachel, Depto Solala, UMMZ 98193; San Andres (14°00'N, 90°04'W), UMMZ 75191; El Reposo (4.2 mi W La Democracia), Depto Huehuetenango, UMMZ 126300.

Population 26. (31:3,11)

GUATEMALA: Nr La Libertad, UMMZ 75189-90, 75192-99, 75200-10.

Population 27. (31:5,20)

CAMPECHE: Balchaca (18°25'N, 91°30'W), FMNH 116488-89, 116491-93, 116496, 116498-500, 116506; Chompoton, UMMZ 73092-73106; Dzibalchen (19°31'N, 89°45'W), KU 75645-47; 23 km W Xpujil, KU 75115; 24.7 mi NE Sabancuy, UMMZ 126439, LACM 61108.

Population 28. (96:48,30)

YUCATAN: Xcach Aguada, vic Izamal (20°56'N, 89°01'W), UMMZ 81541-55; Kanana, 50 km S Merida, UMMZ 81556-61; nr Telchac Puerto, UMMZ 76130-41; Cenote, 0.6 mi E and 1.5 mi S Libre Union, UU 9532-38; Aguada Sayusil, 1.6 mi S Libre Union, UU 9583-639.

Population 29. (23:12,6)

QUINTANA ROO: 10 mi S, 5 mi W Puerto Morelos (20°50'N, 86°52'W), UU 9539-61; Pueblo Nuevo X-can, UU 9580.

Population 30. (17:4,12)

QUINTANA ROO: 5 km N San Miguel, Isla Cozumel (20°25'N, 86°55'W), KU 70932-40; 3.5 km N San Miguel, Isla Cozumel, KU 71770; 5 km S San Miguel, UF 24135, 24141; 6 km S San Miguel, UF 24136; 7 km S San Miguel, UF 24137-39; 9 km S San Miguel, UF 24140.

Population 31. (69:10,28)

BELIZE: Rockstone Pond #1 (17°46'N, 88°22'W), UU 6559-89; Belize (City) (17°30'N, 88°12'W), FMNH 4426, UF 24069-70; 2.9 mi from Belize (City) on airport rd, UF 32624-26; 10 mi E Belize (City) on Belize Cayo Rd, UMMZ 124745.

Population 32. (19:5,12)

EL SALVADOR: San Salvador (13°42'N, 89°12'W), FMNH 65022; Cojutepeque (13°43'N, 88°56'W), UU 7646; Rio Sucio, La Libertad (13°29'N, 89°19'W), UU 7647-48, 7650-59, 7676, 9267; Instituto Tropical D.I.C., UU 7660-62.

Population 33. (9:5,4)

GUATEMELA: Río Sal, Jutiapa Depto Jutiapa (14°17'N, 89°54'W), UMMZ 107114-15; Finca La Trinidad, Depto Jutiapa, UMMZ 107885; Escuipulos, Depto Chiquimala (14°34'N, 89°21'W), UMMZ 107116; Lago de Guija (delta del Anque), Santa Ana (14°17'N, 89°31'W), UU 7641-45.

Population 34. (57:36,21)

HONDURAS: Escuela Agricola Panamericama, Zamorano, F. Morizan (14°00'N, 87°02'W), UU 7634-40, MCZ 49749-50; trib of Yaquaro Zamorano, Tegucigalpa, MCZ 48770-72.

EL SAVADOR: 1 mi NNE La Union turn off at Sirama, La Union, UU 7674-76; Laguna Olemega, San Miguel, UU 7663-73; Monte Cristo Mine, NE San Miguel, La Union, FMNH 65023.

NICARAGUA: Río San Isidro, Chinandega (12°45'N, 87°05'W), UU 7258-86; San Antonio, Chinandega, KU 85530.

Population 35. (233:104,129)

NICARAGUA: 1/2 mi NE Granada, Granada (11°56'N, 85°57'W), UU 7288; Río Tipitapa, 1-1-1/2 mi NE Granada, Granada, 7289-7296; Rio Tipitapa, Los Cocos, Granada (12°05'N, 85°54'W), UU 7309-474; 1 mi E Matagalpa, UMMZ 116560; Rio El Limon, 1-1/2 mi SE La Virgen, Rivas, UU 7246-57; Estero Sto Domingo, Rancho El Morillo, Río San Juan, UU 7208-45; 13 km N Los Maderos, Managua, KU 85529.

COSTA RICA: Mouth of Río Sapoa, Guanacaste, UCR-SAP A-E; 12 km N La Cruz, Guanacaste, CRE 9019.

Population 36. (24:17,7)

COSTA RICA (Guanacaste): Liberia (10°38'N, 85°27'W), KU 46748; 3.9 km SE Liberia, CRE 9891; 5 km N, 4.5 km W Liberia, CRE 105; Hda Coyolar, 3 mi N, 2-1/2 mi W Liberia, CRE 8207; nr Colorado, 5 km NW Río Colorado, CRE 9036; nr Bagaces, CRE 215; Palo Verde, UU 7487-88; 6 mi NE Tilarán, CRE 8020; Río Cañas at Cañas (9°14'N, 83°25'W), CRE 7164; jct Río Cañas and Hwy 21, 12 km N Santa Cruz, UU 7481-83; Río Cañas, 1 mi above Brazilia, UU 7484-86; 11.2 km SE Cañas, CRE 6307; 1-1/2 mi S Hda Mojica, UU 7489-94; Estacion Experimentál Enrique, Jimenez Muñes, LACM 114390.

Population 37. (55:29,20)

COSTA RICA: (Alajuela Province) Hda San Franando, 5 mi W Alajuela (10°01'N, 84°13'W), UU 7476-79; (Puntarenas Province) Finca La Ligita, La Julieta, CRE 8253; 1/4 mi E Boca del Barranca, CRE 8018 (2 specimens); Dominical (90°13'N, 83°51'W), UU 7540, 7542, 7546-7, 7551-57, 7562-73; Lagoon, 1/2 mi SE Dominical, UU 7543, 7548, 7550, 7559; Lagoon, 1.7 mi SE Dominical, UU 7539, 7549, 7560-61; Boca del Rio Dominical, 2 mi SE Dominical, UU 7541; 2.3 mi SE Portalon, UU 7544-45, 7558; (San Jose Province) Alejuelita, 5 mi S San Jose (9°55'N, 84°06'W), UMMZ 79515-22; Curriadabat, CRE 2828; Desamparados (9°54'N, 84°04'W), CRE 2832; Patarra, 4 mi SE Desamparados, LACM 61103-05; Escazu, S Vista Alegre, CRE 173.

Population 38. (45:19,28)

COSTA RICA: (Puntarenas Province) Palmar Sur (8°58'N, 83°29'W), UU 7496, 7505, 7508, 7518, 11873; 0.8 km S, 1 km W Palmar Sur, UU 7495, 7499, 7501, 7503-04, 7506-07, 7509-11, 7513-17, 7519-27, 7529-33, 7535-37; 10.3 km S Palmar Sur, UU 7497-98, 7500, 7502, 7512, 7528, 7534; Buenos Aires, UU 7538.

Population 39. (12:4,7)

PANAMÁ: (Chirique Province) Que Cantarilla, 1/2 mi E Horconcitos (8°19'N, 82°10'W), UU 7574-80; Puerto Escondido, UU 7581; Tolé, UU 7582; Los Torones, nr Remedios (8°14'N, 81°51'W), UU 7583; Rio Fonseca, Pan Am Hwy, UU 7584; Rio Santiago, Guabala, UU 7585.

Population 40. (35:18,17)

PANAMÁ: (Veraguas Province) Isla de Cebaco, KU 96975; 2-1/2 mi N, 6 mi E Espino de Santa Maria, UU 7586-92; (Los Santos Province) Guanico Arriba, KU 108327-28; 2.8 mi SW Sabana Grande, UU 9921; 0.6 mi NE Macaracos, UU 9922-23; Creek 5 mi N Guarare (7°43'N, 80°40'W), UU 7596-97; Coiba Island, USNM 137378; (Herrera Province) Chitre (7°58'N, 80°26'W), UU 9920, FMNH 68111-13; (Cocle Province) Río Anton, El Valle, UU 9919; El Valle de Anton, FMNH 68115; (Panamá Province) Nueva Gorgona (8°33'N, 79°52'W), UU 7918, 9917, 12823-5, 12838-41; Cerro Campana, UU 7603; Rio La Garta, 2 mi NNE Bejuco, UU 7604; Pan Am Hwy nr Penonome (8°31'N, 80°22'W), UU 7593; Cocle, nr Nata, UU 7594.

Population 42. (173:74,93)

HONDURAS: Tomsin, 15 km NW Puerto Lempira, LACM 48440-43, 48445-46; Lempira, 13.5 mi NNW Gracias, LACM 48447.

NICARAGUA: (Gracias a Díos) Cabo Gracias a Díos, UU 4588-99, 7029-30, 7053-95, 7102-76, 7178-7202; Tronquera, Río Lecus, 17 mi SSE Waspan, UU 7046, 7048-50; 2 mi NW Tronquera, UU 7045, 7047; Leimus Creek, Sta Ines, UU 7035.

Population 43. (36:16,20)

NICARAGUA: (Zelaya) Puerto Cabezas (14°02'N, 83°23'W), UU 7014-15, 7017-18, 7025, 7027, 7031, 127251; 2 mi SSW Pto Cabezas, UU 7016, 7019-21, 7032, 12750; 5-1/2 mi NW Pto Cabezas, UU 7022-23, 7026, 7033; 6-1/2 mi NW Pto Cabezas, UU 7024, 7028, 7034; Rio Cuculaya, Isnawas (13°48'N, 83°45'W), UU 7037; Laguna Cuculaya, 5 mi S Isnawas, UU 7036, 7038; 10 mi NNW Auypini, UU 7039-44; Karatá, 7051-52; Celaya, KU 40133; New Found Out, 15 mi NNE Bluefields, UU 7205-07.

Population 44. (13:5,4)

COLOMBIA: San Andres Island (12°36'N, 81°40'W), LACM 38231-9, 38458, 38471-73.

Population 45. (39:25,12)

CANAL ZONE: Panama Railroad, USNM 117369 (holotype); Red Tank (9°00'N, 79°36'W), UU 9925-26, 12524; 1/2 mi ESE Red Tank, UU 7607; 1/2 mi N Red Tank, UU 7608-12; Río Pedro, Red Tank, 4 mi NW Gaillard Hwy, UU 9924; Pedro Miguel Lake, UU 12779, 12862, 12834; nr Ancon, MCZ 18930 (paratype); 0.5 mi N Paraiso, UU 13164; Corozal, UU 9918;

Albrook Field, UU 7613; Ft Kobe, UU 7605; Juan Mina (9°10'N, 79°39'W), UU 7615-18; Gorgona, UU 7598-601.

PANAMÁ: (Panamá Province) Panamá (8°58'N, 79°15'W), USNM 7854 (paratype); nr Old Panamá, MCZ 24957A-24957B (paratypes); nr Panamá, UU 7606; Río Tocumen, 3 mi S Tocumen Airport, UU 7620, 7622-23; Pan Am Hwy, 2.1 mi W Río Pacora, UU 7619, 7621; 3 km SW Naramjal, KU 77700; Transisthmian Hwy, 4 mi N Pueblo Nuevo, FMNH 57624; 9 km NE La Chorrera, UU 7602; Juan Diaz, UU 7614.

Population 46. (8:1,6)

COLOMBIA: Rio Ocoa, nr Villa Vicencio (4°09'N, 73°38'W), FMNH 7343; Mimil, lower Rio Sinu, Cordoba, FMNH 73665-66; Los Micros, San Juan de Arama (4°58'N, 75°52'W), FMNH 81325-27; Río Ariari, Granada, Meta, ?369 (seen at UMMZ); Fundacion, UMMZ 45609.

Population 47. (4:3,1)

VENEZUELA: Between Pto Ocumare and Ocumare de la Costa, Est Aragua, UMMZ 124291-94.

Population 48. (8:5,3)

VENEZUELA: Garacínas, Sucre, WED 39838.

TRINIDAD: Trinidad, UU 10257; Brickfield, FMNH 53654-56; Malibar, Arima, UU 4424; Somgre Grande, UU 4425; vic Arima Valley, UF 16511.

Population 49. (5:2,3)

BRITISH GUIANA: Pomeroon, USNM 84582-85; Dunoon, UMMZ 46675.

Population 50. (11:8,3)

BRAZIL: "Amazon", USNM 65102-04, 85025; Pará, USNM 65662; Belem, Pará, KU 130267-70, FMNH 44251; Marajo Id, Lower Amazonia, USNM 28964.

Population 51. (3:3,0)

BRAZIL: Papery, Río Grande del Norte, FMNH 64252; Pernambuco, Pacao, UMMZ 103242; Serra de Acai, Nun de Pezqueria, Pernambuco, Pacao, UMMZ 115652.

Population 52. (6:2,3)

ECUADOR: Santa Cecilia, Napo-Pastaza, KU 105441-42, 109856, 112228, 155519, 158540.

Population 53. (3:2,1)

PERU: Yarina Cocha, Ucayali, Loreto, FMNH 45665-67.

Population 54. (3:1,2)

ARGENTINA: Embarcacion, Salta, LACM 73984; Jujuy, Yuto, JBI 781-82.

Kinosternon leucostomum Complex

Population A. (83:37,35)

VERACRUZ: Veracruz (19°12'N, 96°08'W), UU 9965, 10258-61, UMMZ 89388, 89390, 89392-93, 118290-93, USNM 109189-92, 109194-96, 109198, 109202, 109205-11; 5 mi SSE Veracruz, KU 47375-76; Alvarado (18°46'N, 95°46'W), UU 8555-62, 8564, 8566-70, 8572-73, 8576-77, 8579, 8581-82, 8585-87, 11875, KU 48972; Río El Limon, nr Alvarado, UU 8563, 8565, 8571, 8574-75, 8578, 8580, 8583-84, 8588, KU 40129-30, 40163-65; Lago de Alvarado, UF 32628-29; 38 km SE Jesus Carranza (17°26'N, 95°02'W), KU 24447; 2 km N Presidco, KU 51448; 4 mi E Encero, KU 51449; 4 mi NNE Minatitlán (17°59'N, 94°31'W), UU 7953-55; 5 km E Cuezalapan (18°22'N, 95°00'W), UMMZ 121140; 41.5 mi S Acayucan, UMMZ 119783.

OAXACA: Río Coatzacoalcos above Sta María Chimalapa (16°55'N, 94°41'W), AMNH 97997.

Population B. (13:8,4)

TABASCO: Purchased in Villahermosa (17°59'N, 92°55'W), UU 11906-07, 12424; Río Tabasquillo, nr Fronterra (18°32'N, 92°38'W), UU 9521-28; 1 mi E Teapa (17°33'N, 92°57'W), UMMZ 119784-85.

Population C. (25:7,12)

CHIAPAS: Laguna de Monte Bello (16°07'N, 91°40'W), UF 24705, UMMZ 129712; Sabana de San Quintin (16°24'N, 91°20'W), KU 94142-43; Palenque (17°31'N, 91°58'W), USNM 108582-86.

GUATEMALA: nr La Libertad (16°47'N, 90°07'W), UMMZ 75223-25; nr Flores, UMMZ 79111; Laguna de Peters, UMMZ 79112; 20 km NNW Chinajá (16°04'N, 90°15'W), KU 55967-68; ± 15 km NNW Chinajá, KU 55969; ± 7 mi WNW Chinajá, KU 55970; vic Finca Chama (23 km N Cobán, 15°30'N, 9°20'W), UMMZ 89585-91; Chinajá, KU 55965, 94149.

Population D. (116:53,63)

QUINTANA ROO: 4 km NNE Felipe Carrillo Puerto (19°35'N, 88°03'W), KU 70941; 9 mi SSE Dziuche (19°54'N, 88°48'W), UU 9520.

BELIZE: Rockstone Pond #1, Belize Dist (17°46'N, 88°22'W), UU 6139-43, 6533-58, 9472-73; 2 mi W Rockstone Pond #1, Belize Dist, UU 9452-71; 50 mi NW Stann Creek Town on Hummingbird Hwy, UF 30373-76; On the Hummingbird Hwy in the mountains, UMMZ 12749; 50 mi from Belize

Cayo Rd on Pine Ridge Rd, 2 mi from Milliamaro Camp, UMMZ 124747; 12 mi S Cayo, Cayo (17°10'N, 89°04'W), UMMZ 70462-64; ca 4 mi SW Cayo, Cayo, UMMZ 124748; Chial, Cayo, UU 9529-30; Augustine Creek, Augustine, Cayo, UU 9478-92; Augustine, Cayo, UMMZ 80705-08; 31.4 mi S Georgeville, Cayo, KU 15764; Valentin, Cayo, UMMZ 80703-04, 80727; Pine Ridge Road, between 36 and 49 mi from Belize-Cayo Rd, UMMZ 124746; Melinda Forest Station (17°00'N, 88°18'W), Stann Creek Dist, UU 9495-519.

GUATEMALA: Tikal, El Peten (17°20'N, 89°39'W), UMMZ 117227-240, UF 13477, 13488; Uaxactum, UMMZ 70465.

Population E. (55:13,15)

GUATEMALA: Panzos, Alta Verapaz (15°24'N, 89°40'W), UMMZ 89592-624; Finca Tinajos, Panzos, Alta Verapaz, BYU 16227; El Astor, Alta Verapaz, BYU 16225; Puerto Barrios (15°43'N, 88°36'W), UMMZ 117804, FMNH 20216, 20218, 20220; Escobas, opposite Puerto Barrios, FMNH 20028; UMMZ 117805-06; Puerto Barrios, Izabal, FMNH 20494-96; Escobas, Izabal, FMNH 20679; Bobos Plantation, Izabal, nr Playitas, FMNH 20114, 20117; Bobos Plantation, Chinamite R, nr Playitas, UMMZ 117807-08; Río Sarquito, Izabal, BYU 16226, 16228; Finca Tesoro, El Guiche, UMMZ 89220-21; Los Amates, FMNH 1888.

Population F. (44:18,26)

HONDURAS: Estero Prieta, Masica, Cortes (15°39'N, 88°07'W), UU 8591-608; Rancho Ustarriz, Tulian, Cortes (15°45'N, 87°57'W), UU 8589-00; Ceiba (15°47'N, 86°50'W), USNM 62981-90; Tela (15°44'N, 87°27'W), MCZ 27911-15, 29125-31; in bayou of Río Bernejo, San Pedro, FMNH 5315; 12 mi ENE Copán, Copán, LACM 48439; 8 mi ENE Copán, Copán, LACM 48437-38.

Population G. (68:34,22)

HONDURAS: 15 mi NW Puerto Lempira, Tansin, Gracias a Díos (15°15'N, 83°54'W), LACM 48432-35.

NICARAGUA: Cabo Gracias a Díos (14°59'N, 83°10'W), UU 9027-84; 2 mi SSW Puerto Cabezas, Zelaya, UU 9111; Rio Cuculaya, Isnawas, Zelaya (13°48'N, 83°45'W), UU 9113; Laguna Cuculaya, 5 mi S Isnawas, UU 9114-16; Bonanza, Zelaya, KU 85521.

Population H. (145:95,41)

NICARAGUA: Corn Island (12°15'N, 83°00'W), UU 9117-254; Isla Grande de Maize, KU 85522-24, 128707-09; Little Corn Island, AMNH 97019.

Population I. (31:16,12)

NICARAGUA: Chihuahua Cr, 2-1/2 mi E El Recreo, Zelaya

(12°10'N, 84°19'W), UU 9085-110; New Found Out, 15 mi NNE Bluefields, Zelaya (12°00'N, 83°46'W), UU 9262-64; Cukra Hill, Zelaya, UU 9260-61.

Population J. (128:65,50)

NICARAGUA: Estero Santo Domingo, Rancho El Morillo, Río San Juan, UU 9255-58.

COSTA RICA: 6 mi NNW Puerto Viejo, Heredia (10°26'N, 83°59'W), UU 4232, 8633-38; jct Sarapiqui and P Viejo Rivers, Heredia, CRE 67; Swamp, Finca La Selva, Heredia, CRE 6446; Moravia, Cartago (9°51'N, 83°26'W), UU 8639-43; Chitaría, Cartago (9°57'N, 83°36'W), KU 104094; 4 mi S Turrialba (9°54'N, 83°41'W), KU 43618-19; IAIA Turrialba, KU 43620; IICA, Turrialba, MCZ 56119-20; UU 8656, 8658; Laguna Bonilla, 1/2 km N Tunnel Camp, UU 8644-48, 8659-60, 8665; nr Peralta, Tunnel Camp, KU 43620; nr Peralta, Lake Bonilla, KU 43621; Finca Escalante, La Roncha, 2.5 km NW Turrialba, UU 8649-55, 8657, 8661-63; Finca Instituto, tunnel, Turrialba, JP-A2-A5; Rio Reventazon, Turrialba, MCZ 54980; Port Limon, Limon (10°00'N, 83°02'W), MCZ 28706-13, 29119-24; La Lola, Limon, UU 8621-32, UMMZ 119495; Los Diamantes, Limon, UU 8667, 8677, KU 31010; Caña Numancia, 7 km N Los Diamantes, Limon, UU 8666, 8669-70, 8672-75; 6-1/2 km N Los Diamantes, Limon, UU 8668; Tontuguero, Limon, MCZ 54996, UMMZ 133262, UF 10300-02, 10498, 10651, 15667-68, 15673; Colonia, 7 km N Guapiles (10°13'N, 83°46'W), UU 8671, 8676; Jimenez, Guapiles, JP-A79; Gaucimo, Limon, JP-A74, A761-A762, A841-A842; 1/4 mi E Valliente, Limon, UU 8612, 8615-17, 8619-20; Caña Negra, 3-1/2 mi ESE Valliente, UU 8609-11, 8612, 8618; Suretka, KU 43623-24; Monte Vade, MCZ 29283-84; Lake Arenal, Guanacaste (10°32'N, 84°56'W), KU 43628, CRE 6258, 6261; Arenal Basin, 6 km NE Tilaran, UMMZ 122635-37, CRE 523; La Laguna de Finca San Bosco, Guanacaste, CRE 6276-1, 6276-2; Silencio de Tilaran, Guanacaste, CRE 6241-A, 6241-C, 6241-D.

Population K. (105:67,31)

COSTA RICA: Suretka, Limon (9°34'N, 82°56'W), KU 43623-24; CLC Railway, mi 26, Limon, UU 8745-46, 8752, 8760, 8778; Daytonia (CLC RR Mi 29.5), Que Cañas Limon, UU 8776.

PANAMÁ (Bocas del Toro): CLC Railway, mi 21, UU 8754, 8769, 8793-94; CLC Railway, 1/2 mi station, UU 9265; CLC Railway, mi 2, Almirante (9°18'N, 82°24'W), UU 12847-60; Que Negra, 3-1/2 mi NW Almirante, UU 8747, 8749, 8751, 8761-62, 8764, 8766, 8770, 8772, 8777, 8780, 8784-85, 8788-89, 8795-99; 1-1/2 mi NW Almirante, UU 8748, 8750, 8753, 8755-57, 8763, 8765, 8768, 8774-75, 8779, 8781-83, 8786-87, 8790-91; 3 km W Almirante, KU 108325-26; Chamquinota, several mi above railroad, UF 21703; Río Occidente, Almirante Bay, UU 8773; Bomana River Station, UU 8758-59, 8767, 8771, 8792; Escudo de Veraguas Island (9°06'N, 81°33'W), UU 8974-78, USNM 148252-56; Cayo Agua Island (9°09'N, 82°02'W), USNM 148268-74, 150027-28; Laguna Tierra, Bastimentos Island (9°18'N, 82°08'W), UU 8960-61, 8963-64, 8966, 8969-70; Shortcut, Bastimentos Island, UU 8962, 8965, 8967-68.

Population L1. (100:64,30)

PANAMÁ: Río Indio, 2 mi upstream from mouth, Colon, UU 8979-83; 3.2 mi S and 1 mi E Piña, Colon (9°17'N, 80°03'W), UU 8951-55, 8958-59; Río Providencia, 4.7 mi S and 1 mi E Providencia, Colon (9°13'N, 80°00'W), UU 8956-57; Achiote, Colon, UU 12781-87, 12794-97, 12835-37.

CANAL ZONE: Canal, UU 13166; H. A. Greene area, Ft. Davis, UU 8984-85, 8987; Ft. Gullick, UU 12788; Escobal, Gatun Lake, UU 12789; Pedro Miguel Lake, UU 12770-78, 12826, 12829-33; Coco Solo R, UU 8973, 12798, 12827; Ammo dump, Coco Solo, UU 8972; Peter McGill River, Chiua Chiua Lake, UU 8910-13; Barro Colorado Island (9°11'N, 79°57'W), UU 8949-50, UMMZ 63734, MCZ 28053, 29132; Stanley Trail, Barro Colorado Island, UU 8947-48; Barbour Trail, Barro Colorado Island, UMMZ 63733-35; Cameron Arm, Miraflores Lake, UU 12790-93, 12801, 12866; Red Tank, UU 9928-35; 1/2 mi N Red Tank, UU 8894-96, 8898-903, 8905-09; 1/2 mi ESE Red Tank, 8897, 8904; Bruja Point, MCZ 24958.

Population L2. (150:101,20)

CANAL ZONE: Gamboa, UU 12802; Río Chagres nr Gamboa (9°07'N, 79°42'W), UMMZ 98361; Que-San Antonio, 3/4 mi NE Gamboa, UU 8888-93; Juan Mina (9°10'N, 79°39'W), UU 8806-87, 8914-46, 9112, 9936-42, 9944, 9946-48, 9950-52, 9954, 9956, 9961, 11876; Río Chilibre, 1/2 mi E Rio Chagres, UU 9943; Río Chilibre, 1000 yds NE Río Chagres, UU 9945, 9949, 9957, 9959; Río Chilibre, 300 yds NE Río Chagres, UU 9953, 9955; Chagres Landing, UU 12803.

Population M. (32:15,13)

PANAMÁ (San Blas Prov.): Ailigandi (9°14'N, 78°01'W), UU 8990-91, 8993, 8996, 8998, 9000-04; Río Suleti, W of Ailigandi, UU 8989, 8994, 9007; Río Suiti, W of Ailigandi, UU 8992, 8997, 8999, 9008-16; Río Inanati, W of Ailigandi, UU 8995; Río Coco, W of Ailigandi, UU 9005-06; Rio Tamnadi, mainland W of Mulatupu, UU 9018-19; Isla Pino, UU 9020-26.

Population N. (7:4,3)

COSTA RICA: San Isidro del General, San Jose (9°22'N, 83°42'W), KU 43625-7; Universidad de Costa Rica, San Pedro de Montes, San Jose, CRE 7241; 1/4 mi E Boca del Barranca, Puntarenas (9°58'N, 84°42'W), CRE 8018A; Tenorio, Guamacaste, KU 43629-30.

Population O. (7:5,1)

COSTA RICA: 10.3 km SE Palmar Sur, Puntarenas (8°58'N, 83°29'W), UU 8678; 7.8 mi ESE Palmar Sur, UU 8679; Finca El Helechales, 15 km NE Potrero Grande, Puntarenas (9°00'N, 83°11'W), CRE 8277; 4.5 km W Rincon de Osa, Puntarenas, KU 102545-47; 2.7 km SW Rincón de Osa, Puntarenas, CRE 3159.

Population P. (1:1,0)

PANAMÁ: nr Chitre, Herrera, FMNH 68114 (questionable locality).

Population Q. (65:15,40)

PANAMÁ: Goofy Lake, ca. 5 mi NNW Tocumen, Panamá (9°05'N, 79°23'W), UU 8680-744.

Population R. (31:10,12)

PANAMÁ: (Darien Province), 2 mi ESE El Real (8°08'N, 77°43'W), UU 8800-05; GML Camp Laguna, UU 4569-71; Rio Tuira at Río Mono, KU 96956-69; Río Chucanaque nr Río Membrillo, KU 107882-83; Río Chucanaque ca 10 km below Río Subcuti, KU 107884, Oxbow Río Candon, 2.5-3.0 mi W of river-mouth, UMMZ 129367-68; Río Tacarcuna, UU 4567-68.

Population S. (12:4,7)

COLOMBIA: Sautata, lower Río Atrato (7°52'N, 77°05'W), FMNH 73672-82; Juana Regina, below San Jose Silverstone de Buey, Choco, LACM 36785.

Population T. (22:14,7)

COLOMBIA: Pizarro, Choco (5°09'N, 77°23'W), FMNH 42807-08, 42811-15, 55906-09, 63904-07; Playa de Oro, Rio San Juan, Choco, FMNH 55905; Andagoyo, Condoto area, UMMZ 121014; Micay (Cauca) Pacific Coast, Boca del Rio, FMNH 78298; Puebla Rica, Sta Cecilia, Caldas, FMNH 55901-03; jct of Rios Arrato and Opogado, vic Opogado, Choco, LACM 72743.

Population U. (17:7,6)

COLOMBIA: San Gil (6°34'N, 73°08'W), UMMZ 74814; Espinal, UMMZ 78309; Tolimaplains, vic of Espinal, FMNH 78297; Muzo, Boyuca, FMNH 69754, 69757-8, 69760; nr Sasaima, ca 70 km NW Bogota (4°59'N, 74°29'W), FMNH 78299-300; Buena Ventura, LACM 61111; Pto Clover, Río Nechi, Antioquia, FMNH 73758-59; Rio Arquía, Finca Chibiqui, Antioquia, LACM 45448-52.